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VOLUME XXIII, 1963

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A REVISION OF THE BARK BEETLE GENUS *DENDROCTONUS* ERICHSON (COLEOPTERA: SCOLYTIDAE)[1]

Stephen L. Wood[2]

Abstract

This taxonomic revision of all known species of *Dendroctonus* is based on an analysis of anatomical and biological characters. Among the anatomical structures found to be of greatest use in characterizing species were the seminal rod of the male genital capsule, the surface features of the frons, and the features of the elytral declivity. Characters of the egg gallery, position and arrangement of egg niches and grooves, and the character and position of the larval mines provided features for field recognition of species that were equal to, if not superior to, anatomical characters.

Following the general discussion and key each of the fourteen species recognized is treated separately, including a synonymy with an extensive list of references, anatomical description of the adult male and female, type locality, hosts, distribution and a description of the life history and galleries. Figures of anatomical parts, gallery systems and geographical distributions are included.

The species treated and their synonymy were: (1) *brevicomis* Leconte (=*barberi* Hopkins); (2) *frontalis* Zimmerman (=*arizonicus* Hopkins, *mexicanus* Hopkins); (3) *parallelocollis* Chapuis (=*approximatus* Dietz); (4) *adjunctus* Blandford (=*convexifrons* Hopkins); (5) *ponderosae* Hopkins (=*monticolae* Hopkins, *jeffreyi* Hopkins); (6) *aztecus* Wood, new species; (7) *terebrans* (Olivier); (8) *valens* Leconte (=*beckeri* Thatcher); (9) *micans* (Kugelann); (10) *punctatus* Leconte (=*johanseni* Swaine); (11) *murrayanae* Hopkins (=*rufipennis* Hopkins, nec. Kirby); (12) *obesus* (Mannerheim) (=*rufipennis* Kirby, *similis* Leconte, *piceaperda* Hopkins, *engelmanni* Hopkins, *borealis* Hopkins); (13) *simplex* Leconte; (14) *pseudotsugae* Hopkins.

[1]This study was supported by a research grant from the National Science Foundation, number B-6532.

[2]Zoology and Entomology Department, Brigham Young University, Provo, Utah. Scolytoidea contribution no. 24.

Introduction

The genus *Dendroctonus* consists of thirteen American species that range throughout the coniferous forests from Guatemala to the northern limits of tree growth in Canada and Alaska, and one Eurasian species that inhabits spruce forests from northern France to Siberia. All species infest coniferous hosts, principally representatives of the genera *Pinus*, *Picea*, *Pseudotsuga* and *Larix*, where their aggressiveness has marked them as the greatest tree killers known. Fantastic losses of standing timber resources, conservatively estimated as averaging more than five billion board feet annually, have resulted from epidemics of these insects.

All species in the genus bore in the inner bark of the bole of the host where they feed primarily upon the phloem tissue. They generally attack only living trees larger than about eight inches in diameter, either standing or prostrate, that have been weakened by age, drought, or other ecological factors; however, vigorous, healthy trees are not immune from attack, particularly during an epidemic. Their success in overcoming a tree is partly due to their gregarious nature, and partly to their association with blue-stain fungi and yeast organisms which interfere with normal physiology of the host thereby assuring success of the bark beetle attack. All fourteen species, with the possible exception of *aztecus*, are widely distributed geographically but are rather limited in host range. All species, with the possible exception of *pseudotsugae* and *valens*, confine their attacks to a single genus of host tree, and usually to a limited group of species within that genus, except during epidemic outbreaks when almost any conifer may exhibit signs of attack.

History

As originally described by Erichson (1836:52), the genus *Dendroctonus* included five species listed in the following order: (1) *Bostrichus micans Kugelann*, (2) *Scolytus terebrans* Olivier, (3) *Dermestes piniperda* Linnaeus, (4) *Hylesinus minor* Hartig, and (5) *Hylesinus minimus* Fabricius without the designation of a type species. Later, Eichhoff (1864:25) divided the group and described the genus *Blastophagus* for *Dermestes piniperda* Linnaeus and *Hylesinus minor* Hartig, and the genus *Carphoborus* (Eichhoff 1864:27) for *Hylesinus minimus* Fabricius. Since that date there has been no question concerning the identity or validity of the name *Dendroctonus* and no synonyms or subgenera have been described. Everyone treating this genus since its description, however, has overlooked the fact that Westwood (1838:39) designated *Dermestes piniperda* Linnaeus as the type species of the genus *Dendroctonus* just two years after its description. Hopkins' (1909:5) designation of *Bostrichus micans* Kugelann as the types species is, therefore, technically invalid.

Latreille (1802:203) described the monobasic genus *Tomicus* with *Hylesinus piniperda* Fabricius, which by definition (Fabricius,

1801:392) was *Dermestes piniperda* Linnaeus, as the type species. Because of an unfortunate error in identification, Latreille's name *Tomicus* became associated with another genus (*Ips* DeGeer) for approximately a hundred years before the error was detected, but the correct usage of Latreille's name was never restored by European writers. Meanwhile, *Dermestes piniperda* Linnaeus was designated as the type species of *Dendroctonus* Erichson (1836) by Westwood (*loc. cit.*), of *Blastophagus* Eichhoff (1864) (nec. *Blastophagus* Gravenhorst, 1827, or *Blastophaga* Gravenhorst, 1829, order Hymenoptera), by Lacordaire (1866:360), and of *Myelophilus* Eichhoff (1878:400) (nec. *Myelophila* Treitschke, 1835, order Lepidoptera). Since all four genera have, by definition or subsequent assignment, *Dermestes piniperda* Linnaeus as the type species, they are objective synonyms of one another with *Tomicus* Latreille having priority by at least 34 years.

By strict application of the Law of Priority the name *Dendroctonus* is unavailable for use in designating the genus to which *Bostrichus micans* and its allies belong. However, because of its unquestioned, consistent usage for more than a hundred years, because of the voluminous published literature concerning it, because of the tremendous economical and biological importance of the species involved, and because the original generic description applies to *micans*, the first species listed by Erichson (with a five-segmented antennal funicle), and not to *piniperda*, the third species listed (with a six-segmented funicle), an appeal was made to the International Commission on Zoological Nomenclature (Wood, 1961) to exercise its plenary powers in order to conserve the name *Dendroctonus* Erichson, with *Bostrichus micans* Kugelann as the type species as designated by Hopkins (1909:5), and to invalidate Westwood's (*loc. cit.*) type designation of *Dermestes piniperda Linnaeus*. The recommended action has now been taken that permanently fixes the name *Dendroctonus* to the genus treated here, with *Bostrichus micans* Kugelann as its type (Opinions and Declarations Rendered by the International Commission on Zoological Nomenclature, Opinion No. 670, in press).

To *Bostrichus micans and Scolytus terebrans* that were included in the original diagnosis of the genus by Erichson, Zimmerman (1868:149) added his new species *frontalis*, and also cited *terebrans*. Leconte (1860:59) described *valens* and *similis* as new species, then later (1868:173) added *Hylurgus obesus* Mannerheim, *Hylurgus rufipennis* Kirby and described as new *punctatus* and *simplex;* he also listed *frontalis* and mentioned *valens* as a synonym of *terebrans*. Chapuis (1869:34) recognized *micans*, *valens*, *obesus* and *terebrans*, and described *parallocollis* as new. Leconte (1876:384-386) listed *terebrans* (=*valens*), *similis*, *rufipennis* (=*obesus*), *punctatus*, *simplex*, *frontalis* and a new species *brevicomis*. Dietz (1890) recognized *terebrans*, *rufipennis* (=*similis*), *simplex*, and *frontalis* (=*brevicomis*) and described *approximatus* as new to the genus. Blandford (1897:146-147) recognized *terebrans* (=*valens*), *parallelocollis*, *approximatus*, and his new *adjunctus*. In many, if not most

of the above citations the specimens under consideration by the various authors did not belong to the species named, and each writer in attempting to clarify the classification of *Dendroctonus* only added to the confusion of species.

In a series of papers published between 1892 and 1909, and summarized in his monumental monograph of the genus, Hopkins (1909) presented a new classification in which he added as new the names *barberi*, *convexifrons*, *arizonicus*, *mexicanus*, *monticolae*, *ponderosae*, *jeffreyi*, *pseudotsugae*, *piceaperda*, *engelmanni*, *borealis* and *murrayanae*. He also recognized as valid the previously described species *brevicomis*, *frontalis*, *parallelocollis*, *approximatus*, *simplex*, *obesus* (=*similis*), *rufipennis*, *punctatus*, *micans*, *terebrans*, *valens* and *adjunctus*.

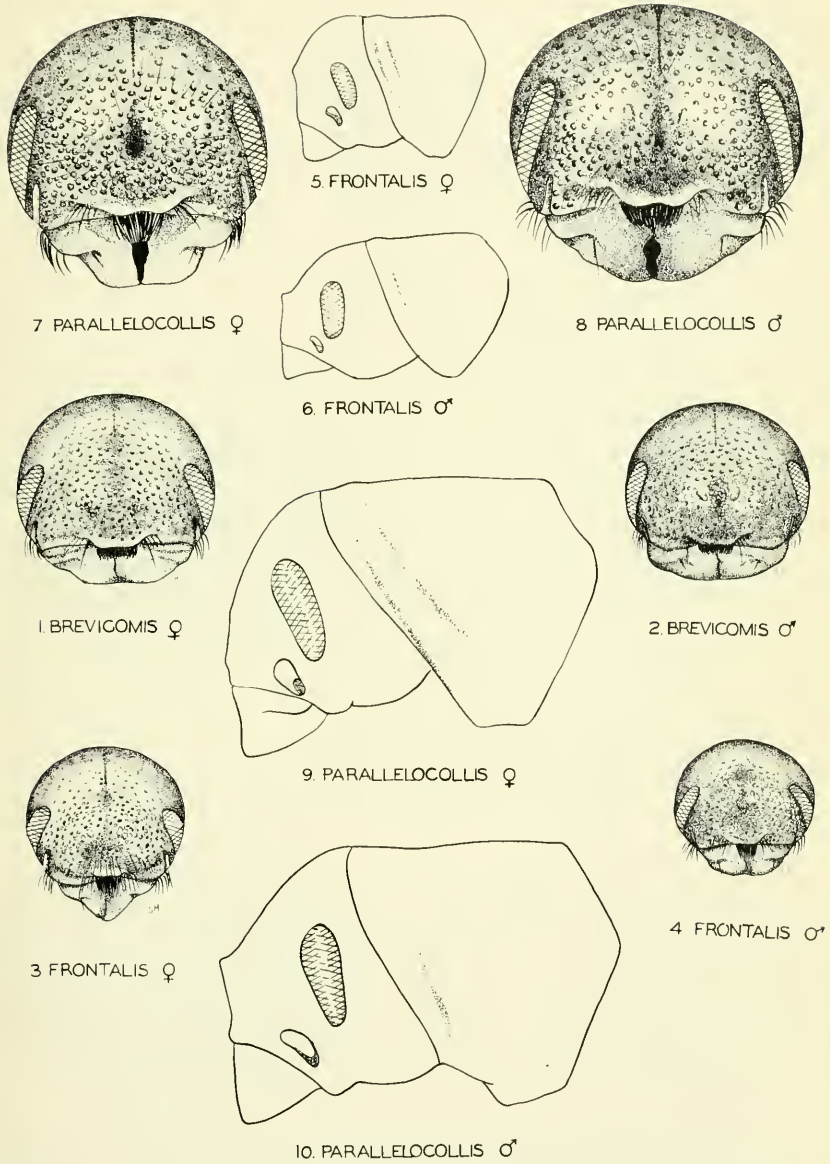
Alterations in the genus since the monograph by Hopkins include the addition of two names, *johanseni* by Swaine (1919:5E) and *beckeri* by Thatcher (1954:4), and the placement of *approximatus* as a synonym of *parallelocollis* by Schedl (1955:11), and of *beckeri* as a synonym of *valens* by Schedl (1955:15).

Discussion of Morphological Characters

General features.—Although characteristic of the various species in a general way, body size could be used only in conjunction with other characters because the smallest specimens of the largest species (*valens*) were almost as small as the largest specimens of the smallest species (*frontalis*). Body form ranged from moderately stout to rather slender, but differences were too slight and individual variation too great to distinguish between any but the extremes of body form. Mature body color was very characteristic of groups of species; for example, the first seven species listed in the key were uniformly black (or very dark brown), *valens* was a distinctive reddish brown, *micans* and *punctatus* a rather dark brown, and the last four species listed were very dark brown with much lighter reddish brown elytra. The vestiture was characteristic of one species only, *brevicomis*, where it was uniformly short.

Head.—The general surface sculpturing of the facial region was of extreme value and provided perhaps the most reliable external characters in establishing a workable classification of the genus. In general, the facial region is convex from the slightly elevated, smooth epistomal margin to the vertex, with a conspicuous epistomal process developed immediately above and overlapping the median portion of the elevated rim of the epistomal margin.

The epistomal process varied in width from a distance equal to one-fourth to one-half the distance between the eyes, with the lateral margins oblique and diverging from its horizontal apical portion towards its base by an angle as small as 20° in males of *valens* (Fig. 15) to one exceeding 80° in *pseudotsugae* (Fig. 23). In *aztecus*, *micans*, *simplex* and *pseudotsugae* the process was either transversely convex or flat with the lateral margins rather sharply rounded.



Figs. 1-4, 7-8. Cephalic aspect of head of *Dendroctonus* spp.: 1, *brevicomis* ♀; 2, *brevicomis* ♂; 3, *frontalis* ♀; 4, *frontalis* ♂; 7, *parallelocollis* ♀; 8, *parallelocollis* ♂.

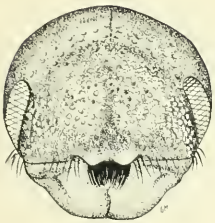
Figs. 5-6, 9-10. Lateral aspect of head and prothorax of *Dendroctonus* spp.; 5, *frontalis* ♀; 6, *frontalis* ♂; 9, *parallelocollis* ♀; 10, *parallelocollis* ♂.

In all other species the lateral arms were variously elevated thereby making the process transversely concave. In almost every species the epistomal process was somewhat wider with the lateral margins or arms, if elevated at all, more prominently elevated in the males than in the females. It should be emphasized that considerable individual variation in the size and shape of the epistomal process was apparent and could often be used with confidence only in combination with other characters.

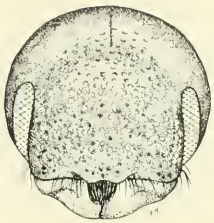
The general contour of the facial region exhibited several consistent and reliable secondary sexual and interspecific variations. For example, in *brevicomis*, *frontalis*, *parallelocollis* and *adjunctus* (Figs. 1-12) a conspicuous median frontal groove below the upper level of the eyes was present with the areas lateral to it rather conspicuously elevated; both the groove and the elevations were more highly developed in the male than in the female. In the males of these species, except in *adjunctus*, the lateral elevations bear one or two dorsomedially directed, enlarged, almost hornlike tubercles. In *valens* (Fig. 16) and, to a lesser degree, in *terebrans* the female has a small median region elevated at the upper level of the eyes. In *punctatus*, *micans* and *murrayanae* there is a feeble median groove which on the lower third of the frons becomes a more or less definite median carina. In *ponderosae* there are remnants of a median groove at the upper level of the eyes and also on the lower half of the frons; in *aztecus* there is often a comparable, almost scarlike remnant of this impression on the lower half of the frons. In perhaps the majority of species the surface sculpturing, such as punctures and granules, appeared to be very slightly coarser in the female than in the male. In *punctatus*, *micans*, *murrayanae* and *obesus* (Figs. 18-21) the most minute details of surface features, the relative numbers of punctures and granules, offer the only really reliable method of separating species without resorting to dissection of the male genital capsule.

The eyes varied conspicuously in the genus from short and oval to long and slender. As illustrated by Hopkins (1909, fig. 15), however, the variation between individuals of the same species is so great that use of the eyes in classification at the species level is virtually impossible. The antennae are also exceedingly variable within a species and, consequently, were not utilized in this classification; this infraspecific variation probably was due more to variation in the way museum specimens dried than to variation in basic structure.

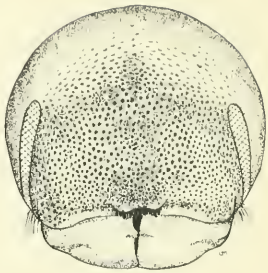
Prothorax.—The outline of the pronotum as seen from the dorsal aspect, although somewhat variable, offers useful characters in classification when used in combination with other features. The basal margin is somewhat bisinuate in all species; the lateral margins are arcuate to varying degrees in the different species and usually more or less converging anteriorly. In *aztecus* (Fig. 25) the transverse constriction just behind the shallowly emarginate anterior margin (Figs. 6, 10) is scarcely visible; in females of *brevi-*



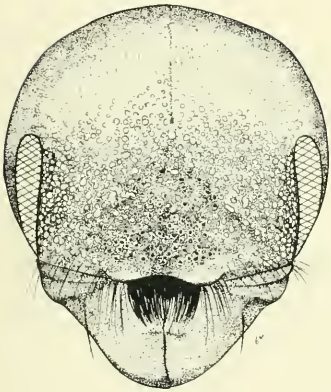
11. ADJUNCTUS ♂



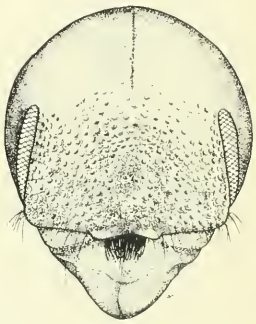
12. ADJUNCTUS ♀



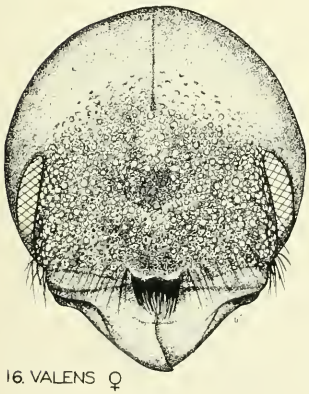
13. PONDEROSAE ♂



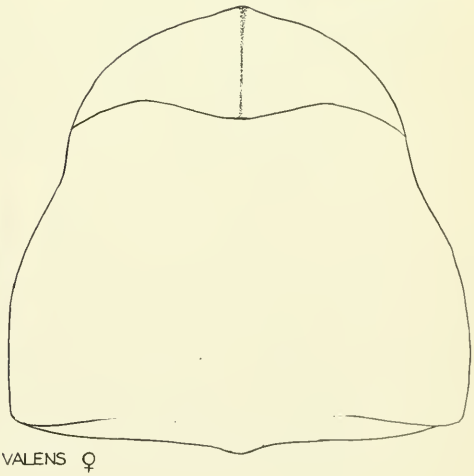
15. VALENS ♂



14. TEREBRANS ♀



16. VALENS ♀



17 VALENS ♀

Figs. 11-16. Cephalic aspect of head of *Dendroctonus* spp.; 11, *adjunctus* ♂; 12, *adjunctus* ♀; 13, *ponderosae* ♂; 14, *terebrans* ♀; 15, *valens* ♂; 16, *valens* ♀.

Fig. 17. Dorsal aspect of head and prothorax of *Dendroctonus valens* ♀.

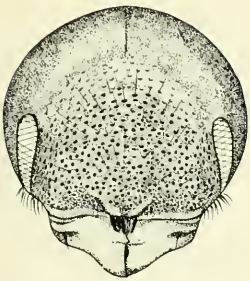
comis, *frontalis* (Fig. 5), *parallelocollis* (Fig. 9) and *adjunctus* the constriction is largely filled by an elevated callus; in the last nine species listed in the key the constriction is rather well developed.

The punctures on the disc of the pronotum vary considerably, both intra- and interspecifically. Because of their variability they were used only sparingly in separating species, this is in contrast to the great emphasis given pronotal punctures by Hopkins (1909:11, etc.). The proepisternal areas vary from punctured with very minute granules to rather coarsely granulate with the punctures almost entirely obliterated. Use of proepisternal characters was made only once in the key, with some reluctance, since the characters are seen with some difficulty unless the proper lighting conditions are employed.

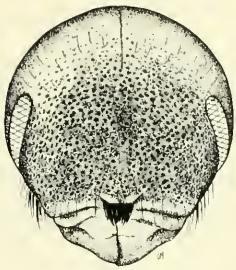
Elytra.—The basic proportions of the elytra vary slightly, but do not reflect characters of value. There also is an increase in the average number of marginal crenulations at the base of each elytron from nine to twelve in the genus. This may have evolutionary significance, but appears too slight and too unreliable to use in diagnosing species.

The elytral striae and interstriae are of considerable value in recognizing species if used with sufficient caution. The interstriae vary from about equal width to more than twice the width of the striae. The striae and strial punctures vary somewhat in depth, but this feature is rather unreliable since lighting conditions may completely change the appearance of this character. The sculpturing of interspaces is rather variable within the genus and usually provides reliable characters for species diagnosis. In only one species, *simplex*, were simple, non-granulate interstrial punctures apparent on the disc. In *aztecus* some of the transverse crenulations on the disc were so coarse and long that they extended across striae and interstriae alike; in most of the species these crenulations varied within definite limits and were very useful when used with other characters in determining species.

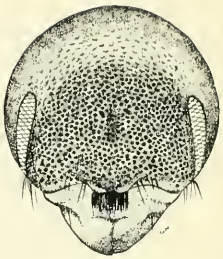
Although conservatively sculptured the characters of the elytral declivity are, in many cases, the most easily observed and reliable external features available for the diagnosis of species. In *brevicomis* and *frontalis* (Figs. 27, 28) the second striae are straight and the second interspace is as wide as one and three; in *simplex* and *pseudotsugae* the second interspace is gradually narrowed and on at least the lower half is narrower than one or three; in all other species the second striae curve toward the suture at least near the elytral apex, causing an abrupt tapering of interspace two on less than the lower fourth of the declivity (Figs. 29, 30). Interspace two is at least shallowly impressed except in *frontalis*, *aztecus*, *murrayanae*, *punctatus* and *micans;* the first interspace is very strongly elevated in *simplex* and *pseudotsugae*, and rather weakly to not at all raised in the other species. The size of strial punctures and the sculpture of interspaces on the declivity usually are characteristic of species and offer excellent characters for diagnosis. In *obesus*,



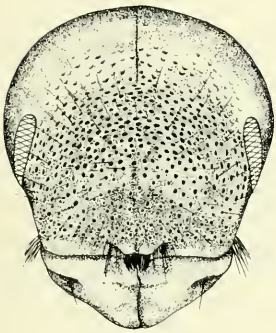
18 PUNCTATUS ♀



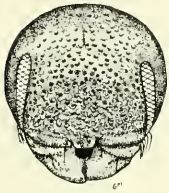
19 MURRAYANAE ♀



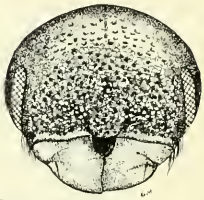
20. OBESUS ♀



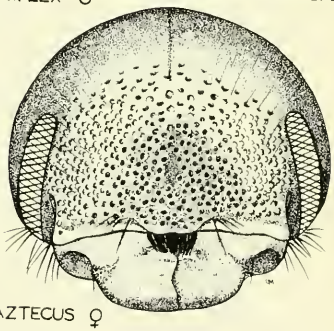
21. MICANS ♀



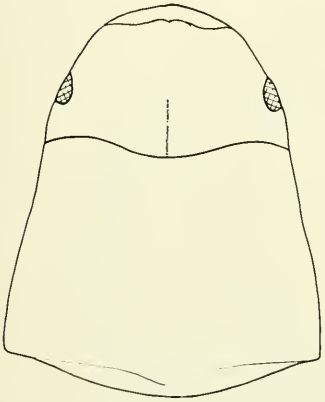
22. SIMPLEX ♂



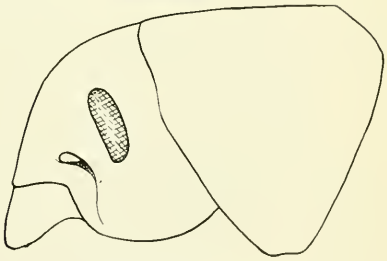
23. PSEUDOTSUGAE ♂



24. AZTECUS ♀



25. AZTECUS ♀



26. AZTECUS ♀

Figs. 18-24. Cephalic aspect of head of *Dendroctonus* spp.: 18, *punctatus* ♀; 19, *murrayanae* ♀; 20, *obesus* ♀; 21, *micans* ♀; 22, *simplex* ♂; 23, *pseudotsugae* ♂; 24, *aztecus* ♀.

Figs. 25-26. Head and prothorax of *Dendroctonus aztecus*: 25, dorsal aspect; 26, lateral aspect.

murrayanae, *simplex*, *pseudotsugae*, and to a lesser extent in other related species, the interstrial granules on the declivity were greatly reduced or absent in the male, thereby providing a convenient, although not entirely reliable, means of distinguishing the sexes.

Legs.—The legs are rather characteristic of the genus, but present no consistent variations of sufficient magnitude to be useful in classification.

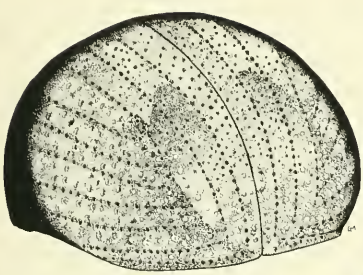
Male genitalia.—Although not suitable for rapid field identification, the characters of the genitalic capsule of the male (Figs. 31-42) included, in several cases, the only truly dependable method for recognizing species. When this study was initiated it was considered virtually impossible to separate *murrayanae*, *obesus*, *micans* and *punctatus* or to find sufficiently reliable evidence to place some of Hopkins' names in synonymy, because of the apparently tremendous individual variation involved, until genitalic characters were studied. When this was done the seemingly incomprehensible mass of variation fell into orderly patterns and very minute characters, particularly on the frons and declivity, which had been meaningless before, became useful and reliable means of diagnosing difficult species. The structure having taxonomic value was designated by Hopkins (1915:118) as the seminal rod.

Generic features.—Of the genera known to the writer, *Tomicus*, *Hylurgus*, *Pachycotes* and *Hylurgonotus* appear to be more closely allied to *Dendroctonus* than others. They share the symmetrical, more or less flattened antennal club; the finely faceted, entire eye; the absence of a presternal ridge between the coxae and the anterior margin of the prothorax; the bilobed third tarsal segments; the hairlike vestiture; and many other characters. In *Pachycotes* and *Hylurgonotus* (*brunneus* only) a distinct, though poorly developed epistomal process is evident, but both have the posterolateral ridge extending along the mandible acutely elevated; the other genera lack both characters; although the mandibular modification is apparent in *Hylurgus*. The male frons is noticeably impressed above in *Pachycotes*, *Hylurgonotus* and *Hylurgus*, almost imperceptibly so in *Tomicus*, and not all impressed in most *Dendroctonus*.

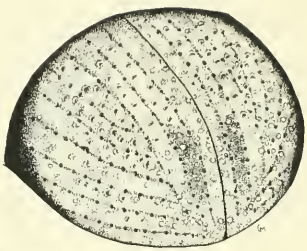
Discussion of Biology

Biology.—All species of *Dendroctonus* may pass the winter in almost any stage of development, however, some species are represented by a preponderance of one stage. In *adjunctus* and *ponderosae* the larval stage predominates, and in *simplex*, *pseudotsugae*, *terebrans* and perhaps *valens* the adult is the principal overwintering stage. In the other species one stage may be represented more commonly in hibernation than another, but not as disproportionately as those mentioned.

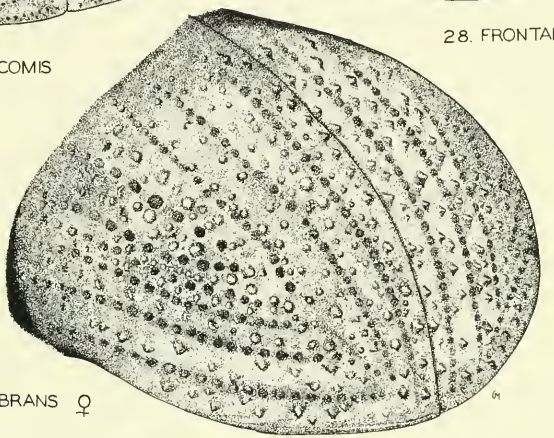
Flight activity for most species begins in the spring whenever daytime temperatures reach about 45° to 50°F., usually about April or May, and continues more or less without interruption until



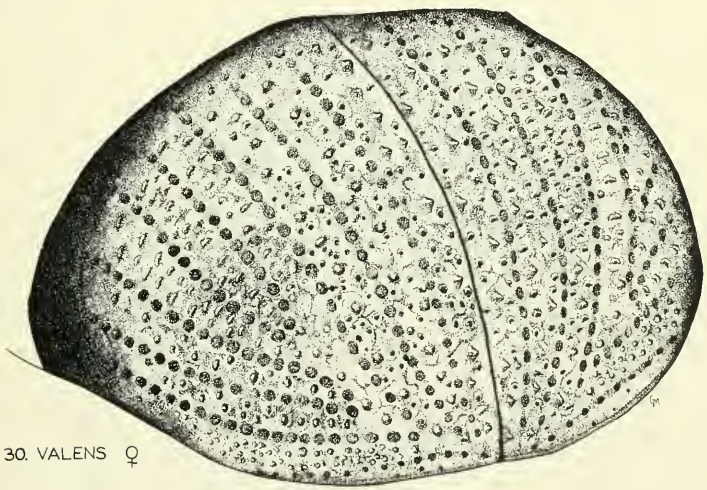
27. BREVICOMIS



28. FRONTALIS



29. TEREBRANS ♀



30. VALENS ♀

Figs. 27-30. Dorsolateral aspect of elytral declivity of *Dendroctonus* spp.: 27, *brevicomis;* 28, *frontalis;* 29. *terebrans* ♀; 30, *valens* ♀.

late September or October. There are, however, conspicuous periods of increased flight activity that correspond with the emergence of overwintered young adults and of each new generation during the summer months. A notable departure from this usual pattern occurs in *ponderosae* where emergence ordinarily does not begin before late July and subsides by mid-September.

All species may, on occasion, attack standing, vigorous trees. Under normal endemic conditions, however, some species, noteably *parallelocollis*, *valens*, *terebrans*, *murrayanae*, *micans*, *punctatus*, *obesus*, *simplex* and *pseudotsugae*, prefer stumps or prostrate trees or logs. Others, such as *bervicomis*, *frontalis*, *adjunctus*, *ponderosae*, and possibly *aztecus*, seldom are found anywhere except in standing trees. Under endemic conditions the standing trees selected for attack ordinarily are either overmature, unthrifty, or weakened by disease, lightning, drought or other factors.

The pattern of attack on a particular standing tree usually is characteristic of the species. For example, *parallelocollis*, *valens*, *terebrans*, *murrayanae*, and possibly *punctatus* and *aztecus* ordinarily confine their attacks to the basal portion of the tree, seldom striking higher than two or three feet above the ground level. In *adjunctus*, *micans*, *obesus* and *ponderosae* (except on mature large trees) the attacks begins on the lower third of the bole and progresses upward; in *brevicomis*, *frontalis*, *pseudotsugae*, possibly *simplex*, and *ponderosae* (at least in overmature sugar pine) the attack begins in the upper midbole area and progresses upward and downward from that point. The attack, depending on the beetle population in a given area, may be concentrated into a few days, or it may extend over more than a year and involve two or more successive generations in some species if competing species do not occupy the available bark.

The individual attack is made by the female usually in a crevice of the bark. When the inner bark is reached and resin ducts are severed the tunnel may be invaded by quantities of pitch that must be removed as the burrow advances. The ability of the female to cope with this material is remarkable. The pitch and frass resulting from the excavation are pushed out of the entrance hole where they adhere to the bark forming a characteristic pitch tube. The presence of these pitch tubes or scattered frass ordinarily is the first indication that the tree is under attack. The size, color and general character of the pitch tubes may indicate the species of beetle making the attack.

Normally, about the time or shortly after the female reaches the phloem tissues she is joined by a male. If the male does not appear the gallery may be advanced, complete with egg niches or grooves until he does arrive, or it may be abandoned and a new attack started. Mating evidently first occurs within a few hours after the phloem tissues are reached; it evidently occurs in the first two or three centimeters of gallery where the gallery is shaped differently and wide enough to permit mating. Mating evidently oc-

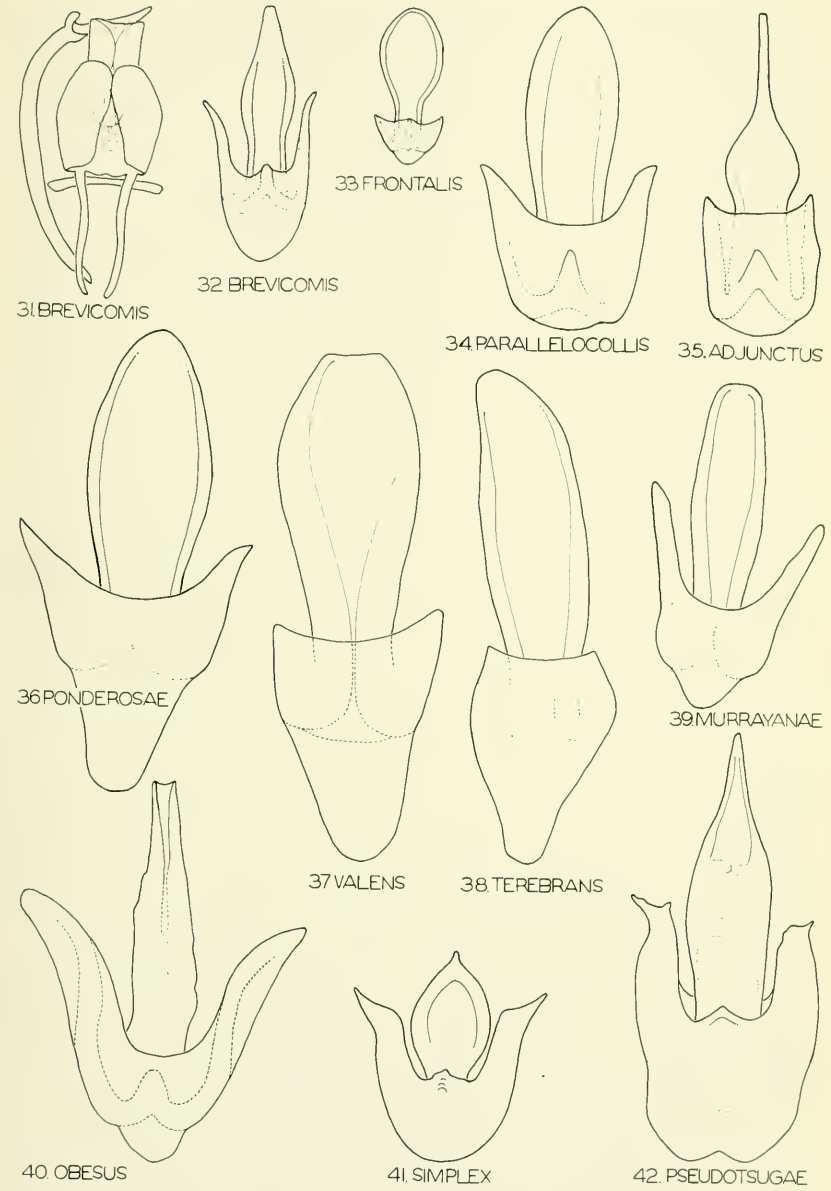


Fig. 31. Dorsal aspect of male genital capsule of *Dendroctonus brevicomis* with the internal position of the seminal rod indicated (posterior end up).

Figs. 32-42. Seminal rod of *Dendroctonus* spp.: 32, *brevicomis*; 33, *frontalis*; 34, *parallelocollis*; 35, *adjunctus*; 36, *ponderosae*; 37, *valens*; 38, *terebrans*; 39, *murrayanae*; 40, *obesus*; 41, *simplex*; 42, *pseudotsugae*.

curs repeatedly, since during this study it was observed in five species in galleries more than half complete. Following mating the male may abandon the gallery in search of another female, but more commonly he remains and takes over the function of removing frass and pitch from the tunnel, thereby permitting the female to concentrate on extension of the gallery and egg deposition. After the gallery is fairly well advanced the frass is packed in the lower or older regions of the gallery thereby closing the entrance tunnel. At any time during the development of the gallery the male may abandon the gallery by extending a ventilation tunnel, or he may remain until death. The female also may remain until death, or she may emerge from the completed gallery and make a second or even a third attack.

There is considerable variation in the character of the egg galleries among the various species of *Dendroctonus*. All are formed in the phloem tissues and scarcely, if at all, engrave the wood. In general they are more or less straight, linear, and follow the grain of the wood; however, in *brevicomis*, *frontalis*, *parallelocollis*, and *adjunctus* (Figs. 46, 47, 49, 51) they are strongly sinuate. In *brevicomis* the total lateral displacement[3] of a gallery usually is equal to or greater than the total longitudinal displacement; the whole complex forms an intertwining network of winding, branching galleries (Fig. 43). In *frontalis* the pattern is very similar to that of *brevicomis*, except that the total longitudinal displacement of one gallery usually exceeds its lateral displacement. Basically the galleries of *parallelocollis* are sinuate, forming a coarse branching and anastomosing criss-cross pattern entirely peculiar to this species. In *adjunctus* the total longitudinal displacement of a gallery is about three to four times greater than the lateral dispalcement; each successive curve, following the first large one, becomes smaller until the final part of the gallery may be virtually straight. In *valens* (Fig. 56), and to lesser extent in *terebrans*, certain parts or perhaps all of the gallery is expanded into a broad, flat cave from which the larvae mine, in congress, thereby enlarging the cave to an area that may cover several square feet of bark surface.

Placement of the eggs along the sides of the gallery varies considerably in the genus. In *brevicomis*, *frontalis*, *parallelocollis*, *adjunctus* and *ponderosae* the eggs always are placed individually in niches that are constructed alternately on the sides of the gallery. In *ponderosae* (Fig. 53) instead of individual niches alternating, from one to eight niches are formed on one side of the gallery then a comparable number are formed on the other. In *parallelocollis* (Fig. 49) the niches are formed in the sides of the gallery farthest from the cambium; the other four species mentioned above place

[3]Lateral displacement refers to deviations from or toward the main vertical axis of a gallery. For example, if the first turn of an egg gallery extends four centimeters to the right, then curves back to the imaginary vertical axis, the total displacement of that turn would be eight centimeters. If this gallery continued three centimeters to the left of the central axis and returned in making a second curve, the total lateral displacement of both turns would then be eight plus six, or 14 centimeters. Longitudinal displacement may be calculated in a similar manner by using a horizontal axis instead of a vertical one.

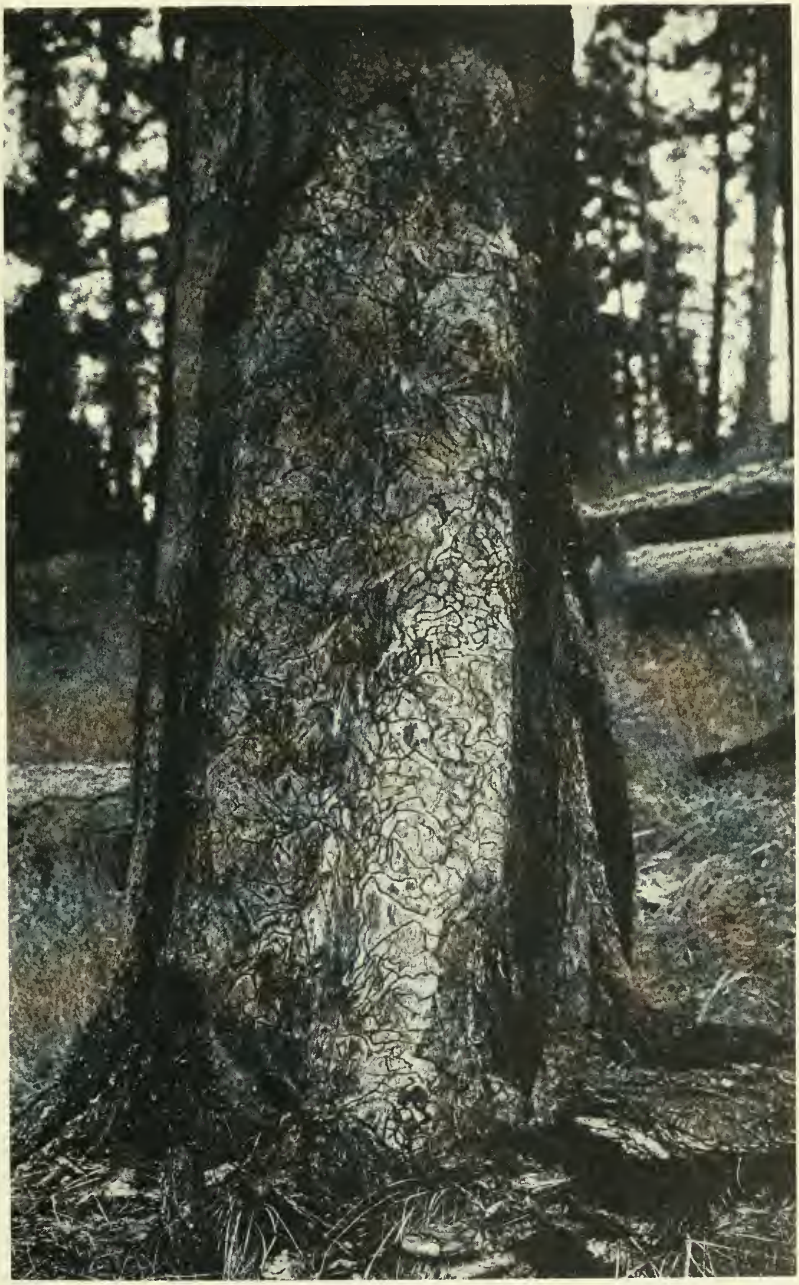


Fig. 43. Dead Ponderosa pine with bark peeled to expose egg galleries of *Dendrotconus brevicomis* (after Swaine, 1914).

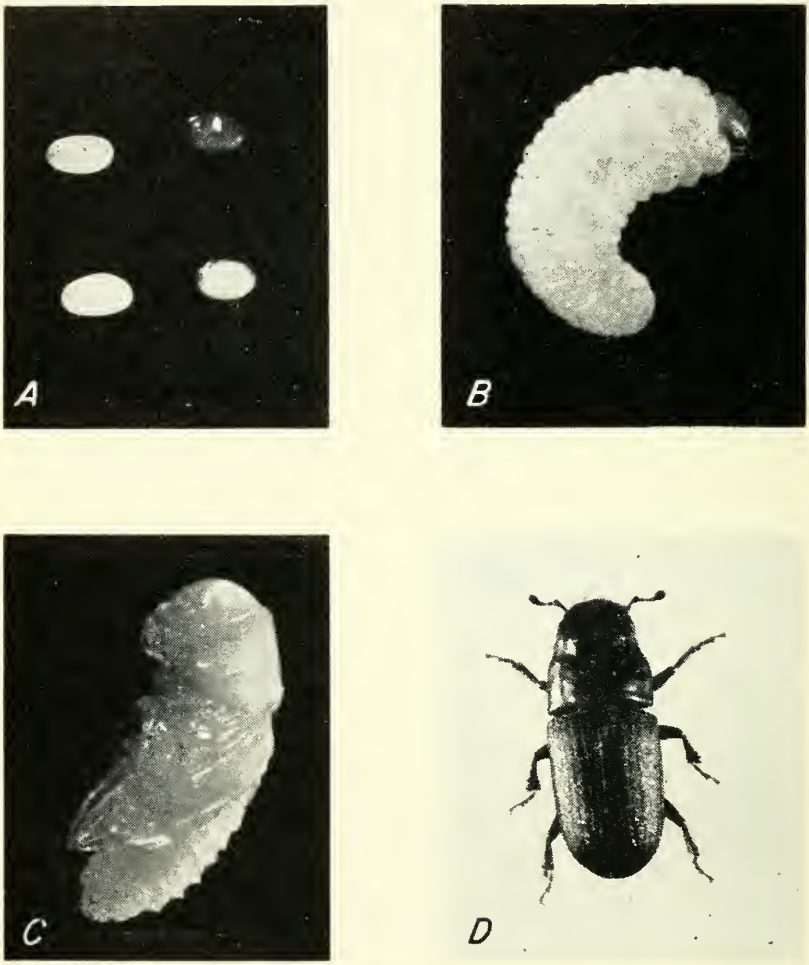


Fig. 44. Stages in the development of *Dendroctonus brevicomis*: A, eggs; B, larva; C. pupa; D, adult (after Miller and Keen, 1960).

their niches next to the cambium (Figs. 46, 47, 51, 53). The remaining species deposit their eggs in masses of about 20 or more in specially prepared grooves along the sides of the gallery. Ordinarily these grooves are placed alternately along the sides. In *pseudotsugae* (Fig. 63) and possibly in *simplex* (not observed), the eggs in each mass are oriented in a definite way; this habit of orienting or placing each egg in a special position did not appear to occur in other species. In *obesus* (Fig. 61) the characteristic habit was to place egg masses in grooves, but frequently some or even all of the eggs in a gallery were placed in individual niches; evidently this occur-

red most often when the beetle encountered unfavorable environmental conditions. The habits of *aztecus* were not observed.

The pattern of larval mines also varied among the different species in the genus. In *brevicomis*, *frontalis*, *parallelocollis*, *adjunctus* and, perhaps to a lesser extent, *ponderosae* and *simplex*, the larval mines are separate from one another and increase only slightly during the first and second instars. They then expand suddenly into an irregular feeding area where the last two larval instars occur. In *parallelocollis* (Fig. 49) the entire larval mine is between the inner and outer bark and is not exposed on the surface of peeled bark. In *brevicomis* (Fig. 46) and in about half of the *frontalis* (Fig. 47) mines the slender initial part of the larval mine is in contact with the cambium and exposed on peeled bark, the expanded portion in both species always is concealed in the inner or outer bark. (except *frontalis* in thin bark). In *adjunctus* (Fig. 51) and *ponderosae* (Fig. 53) the entire larval mine is in contact with the cambium and is exposed on the surface of peeled bark. In *terebrans*, *valens*, *micans*, *punctatus*, *murrayanae* (Fig. 59) and *obesus* (usually) (Fig. 61) the larvae feed in congress, forming a common cave for at least part of the larval period. In *terebrans* and *valens* this communal feeding continues until pupation, except for an occasional larva that forms a short individual tunnel just before pupation. In *murrayanae*, and presumably in *punctatus* and *micans*, the larvae feed in congress for six or eight centimeters when individual groups separate then later rejoin one another leaving islands of unexcavated bark in the feeding area; they may cover considerable distances in the process, but usually the larvae are in a common area by the end of their development. In *obesus* (Fig. 61) the larvae mine in congress for about the second and third instars when each separates from the others and constructs a separate mine, unless crowding is severe. In *pseudotsugae* (Fig. 63) the larvae construct individual mines that increase in width gradually throughout their length.

Pupation in all *brevicomis*, *frontalis* and *parallelocollis*, and in some *adjunctus* and *pseudotsugae*, takes place in the outer bark; in the remaining species it occurs at the end of the larval mine or in the frass of the common feeding chamber in the area of the cambium and is exposed on peeled bark.

The only species known to have a special overwintering habit is *obesus*. About half of the young adults emerge from the brood galleries and re-enter the base of their own or another brood tree or other suitable tree where they construct feeding tunnels. They emerge the following season to commence their attacks on new trees to begin another generation. This habit has not been reported in other species, but is suspected in *murrayanae* and perhaps in one or two other closely related species.

The number of generations each year varies from one to five or more. In *brevicomis* and *frontalis* three or more generations are common in the southern parts of their distributions, with fewer genera-

tions in cooler areas. In the other species one generation and a partial second generation is typical, except in the extreme southern areas where cool temperatures do not interrupt development, or in northern areas where one summer is not sufficient to complete larval development. In *ponderosae* one generation each year appears to be the rule in all areas, except in southern California where two and a partial third generation may occur.

Host specificity.—Under endemic conditions each species of *Dendroctonus* characteristically restricts its attacks to certain preferred species of coniferous trees. Each of the 14 species includes more than one host species in its preferred list; only two infest more than one host genus. Eight species normally attack only trees of the genus *Pinus;* these are *brevicomis*, *frontalis*, *parallelocollis*, *adjunctus*, *aztecus*, *ponderosae*, *terebrans* and *murrayanae.* Three species attack only trees of the genus *Picea;* these include *micans*, *punctatus* and *obesus.* One species, *simplex*, prefers only the species of *Larix.* The species of *Pseudotsuga* are preferred exclusively by *pseudotsugae*, except in northeastern British Columbia where *Larix* evidently is a normal host of endemic populations. The most unrestricted species in the genus is *valens;* it occurs most commonly in species of *Pinus*, but also is found in *Picea*, *Larix*, *Abies* and perhaps other genera of coniferous trees.

A phenomenon that has caused considerable controversy in the past and probably will continue to do so in the immediate future, occurs in several species. It is best illustrated by the distinctive, easily recognized *pseudotsugae.* Over most of its range the only host of this species is Douglas fir; understandably, it may also attack Big Cone spruce, *Pseudotsuga macrocarpa*, in areas where that host occurs. In northeastern British Columbia endemic populations evidently breed successfully in *Larix occidentalis*, although they presumably are unable to do so where both Douglas fir and Western larch occur together in other parts of the beetle's distribution. In *murrayanae* a similar situation presumably occurs in the Great Lakes area where Red pine (*Pinus resinosa*) and Eastern white pine (*Pinus strobus*) apparently are acceptable hosts of endemic populations; in all other parts of its distribution Jack pine (*Pinus banksiana*) or the virtually identical Lodgepole pine (*Pinus contorta*) are the only hosts. It is not impossible in this instance, however, that the Red pine and Eastern white pine infestations resulted from the overflow of an epidemic of this beetle in neighboring Jack pine. A similar, but much more complex problem appears to occur in *ponderosae.*

In *ponderosae* local endemic populations may exhibit a preference for any one of several hosts even though more than one of those on the preferred list may occur in mixed stands with the one actually selected in that area. For example, in certain parts of California Jeffrey pine (*Pinus jeffreyi*) is selected; in parts of Oregon and Washington it may be Western white pine (*Pinus monticola*); in parts of Idaho, Montana, Wyoming and Utah it may be Lodgepole

pine; in parts of Colorado, Utah and the Black Hills it may be Ponderosa pine (*Pinus ponderosa*); in parts of Colorado, Utah, New Mexico and Arizona it may be Pinon pine (*Pinus edulis*); etc. Whether these preferences result from genetic differences in the local beetle populations, from competition between species attempting to occupy the same ecological niche, from differences in the host species, from differences in climate, or from other factors is uncertain. Experienced forest entomologists disagree concerning the behavior of endemic populations of this species in mixed stands of two or more of the preferred hosts. For example, it was reported by reliable, experienced workers that outbreaks of this species in Jeffrey pine did not spread into neighboring stands of Ponderosa pine. Other workers of equal reliability and experience reported that approximately equal numbers of the two host species were attacked when they occurred in mixed stands but that tradition required them to attribute the Ponderosa attacks to *Dendroctonus brevicomis*. Personal investigations conducted for very brief periods at each of three widely separated localities in the area in question, in three different seasons, have led me to the following conclusions for this particular area of controversy. First, in pure stands of Ponderosa pine at the lower elevations *ponderosae* ordinarily is not present, all beetle-killed trees appeared to be occupied by *brevicomis*; in pure stands of Jeffrey pine at higher elevations *ponderosae* has no competition from other aggressive species of *Dendroctonus* and, consequently, is present in all beetle-killed trees. At the higher elevations where mixed stands of the two hosts occurred both were attacked with approximately equal frequency by *ponderosae*, *brevcomis* occasionally was present in some of the Ponderosa pine trees. At the intermediate to lower elevations, rather near mixed stands of these hosts, both species of *Dendroctonus* occurred in the same Ponderosa pine trees, but *ponderosae* evidently occurred only in the lower third of the bole where its galleries were intermixed with those of *brevicomis*. It appeared that the colder winter temperatures encountered at the upper elevations, where mixed stands occurred, were a definite factor in retarding the development of *brevicomis* sufficiently that *ponderosae* could compete successfully in Ponderosa pine. At the lower elevations where mixed stands occurred it appeared that the temperature advantage enjoyed by *ponderosae* was absent and that the only reason this species was represented in Ponderosa pine at all was the nearby reservoir of Jeffrey pine where it enjoyed freedom from competition. In this area of California climatic factors appeared to be much more important than genetic factors. The principal California area considered here was in Lassen National Forest from Old Station to Black's Mountain south to Lassen Park; the elevation varied from about 3200 to about 7000 feet.

In the Uinta Mountains of Utah pure stands of Lodgepole pine occur in certain areas and pure stands of Ponderosa pine occur in others. Between the pure stands are areas where mixed stands of these trees are found. In the absence of usable published data, personal communication from local rangers and other Forest Service

personnel familiar with the area indicate that some outbreaks of *ponderosae* occur in Lodgepole, but not in Ponderosa pine, and that other outbreaks occur in Ponderosa, but not in Lodgepole pine. Other workers reported that these outbreaks ordinarily sweep from one host species to the other. It was also reported that an attempt was made to rear beetles coming from one host species on the other host species, but was unsuccessful. Whether the failure resulted from genetic differences of the beetles or from faulty experimental procedure is unknown. Personal studies in these mixed stands indicated that beetles developing in an area where a mild outbreak in Lodgepole was in progress, were attacking Ponderosa pine. It appeared that a physiological adjustment requiring one or two successive generations was necessary before the normal survival rate of the brood was attained. The rate of survival of brood in the first Ponderosa pine trees attacked in this area was very low.

The above three paragraphs, although intentionally improperly documented to protect confidences, presents a phenomenon not adequately investigated; that is, host-restricted races may arise and behave as species in many respects. These possibly arise when temporarily altered factors of ecology, genetics, or other factors, permit the invasion of a host species different from that normally occupied in a given area. Whether this comes about from relaxed competition, from relaxed resistance of the host, or from other opportunities, the resulting gene flow from one population to another has the effect of preventing species formation. To effectively prevent species formation this need not occur more than once in numerous generations, nor must it occur in more than a few areas within the total distribution of the beetle species. The above example involving *pseudotsugae* appears to be a clear-cut example of a change in host selectivity. The lack of uninimity of opinion as to what occurs in populations of the apparently host-restricted races of *ponderosae*, particularly in view of my Uintah Mountain observations and the apparent absence of anatomical indicators of genetic change throughout its range, suggests a fertile field of research.

Infraspecific Variation

Morphological differences between species in *Dendroctonus* are, at best, rather poor and when complicated by tremendous individual variation the identification of specimens is made exceedingly difficult. Because of this, greater dependence in past years has been placed on locality and host data by specialists in identifying species than on specimens themselves. An analysis of this supposed hopelessly chaotic assemblage of variability appeared impossible until the reliability of genitalic characters in the male was established. Once their reliability was established genitalic characters served as a basis for sorting individual, sexual and geographic variations into comprehensible, predictable patterns and made possible the grouping of several populations, previously regarded as distinct, into recognizable species.

Individual Variation.—The greatest degree of individual variation was in size. Although it was actually demonstrated in only a few species it appeared that the largest specimen found in a particular species was almost exactly twice as large as the smallest specimen examined in that same species (2.5 and 5.0 mm. in *brevicomis*; 2.3 and 4.5 mm. in *frontalis;* 3.7 and 7.5 mm. in *ponderosae*; etc.). The size differences mentioned here possibly result from unusually favorable or unfavorable environmental conditions rather than genetic or other factors; in the three examples cited the largest and smallest individuals came from the same geographical area. Other variations in epistomal processes, antennae and eyes were treated and illustrated by Hopkins (1909:19-23) and were either avoided because of unreliability or were described in the systematic treatment of each species on the following pages.

Individual variations of present concern include usually reliable characters of taxonomic value that occasionally are altered or entirely missing in certain specimens. For example, the male declivity of *valens* ordinarily bears numerous fine, confused granules, but in an occasional specimen (fewer than five precent of the males) only a few median granules are present on each interspace with the locations of others marked by deep punctures. In other cases, an otherwise normal female of *obesus* (about two or three per cent) will have the punctures of the declivital striae two or three times as large as the interstrial punctures; and in males of *murrayanae* (about five percent of those from the west) the interstrial punctures of the declivity may be as much as half as large as the strial punctures. When odd examples such as these are encountered accurate identification may be possible only when they are associated with a long series of normal specimens.

Sexual Variation.—Secondary sexual characters are conspicuously developed in the species of *Dendroctonus*. As with most other genera in the subfamily Hylesininae, the posterior margin of the seventh abdominal tergum in the male bears a pair of closely set median stridulating processes that work against the roughened adjacent surface of the elytra. The squeaking noise of stridulation heard when a specimen is held next to the ear is a convenient field method of identifying males of all species in the genus. The absence of stridulation does not necessarily mean the specimen is a female, since males cannot always be induced to stridulate.

In *brevicomis*, *frontalis*, *parallelocollis* and *adjunctus* the frons has a median groove with the lateral areas elevated. This groove and the lateral elevations are much more highly developed in the males of these species than in the females and, in all but *adjunctus*, the lateral elevations of the males bear one or two pair of large, almost hornlike tubercles on their dorsomedian margins. In these same species the well developed transverse constriction found just behind the anterior margin of the pronotum in the male is largely filled by a conspicuously elevated transverse callus in the female (Figs. 5, 9). In *valens* (Fig. 16) and, to a lesser extent, in *terebrans*, the

female frons bears a small, rather well developed median elevation at the upper level of the eyes. In all six species mentioned above, and other related species, the male frons is usually a little larger and more prominent and the female frons, pronotum and elytra are very slightly more coarsely sculptured.

In *pseudotsugae*, *simplex*, *obesus*, possibly *valens*, and to a much lesser extent *ponderosae*, *micans*, *punctatus* and *murrayanae*, the declivital tubercles on the elytra are moderately large in the female and smaller to entirely absent in the male. Field use has been made of this character in *obesus* giving about 90 percent accuracy; these tubercles would be much more reliable in determining the sex of *pseudotsugae* and *simplex*.

Geographical Variation.—Geographical variation was detected in five species. In each instance Hopkins (1909) employed these variations to characterize new species. Since they are minor, difficult to measure, and involve a minority of the population in any given area they were not used here to characterize geographical races.

Body size varied conspicuously in *ponderosae;* in general, specimens from the northwestern parts of its distribution (Washington and British Columbia) were distinctly smaller than those from the southern areas, particularly the southeastern parts of its distribution. However, there was a gradual transition in size through Idaho, Oregon and northern California. This variation was somewhat obscured by an ecological complication, since thin-barked pines which predominate as hosts of this species in the northwest normally produce smaller beetles than do hosts with thick bark. Size variations of less than one millimeter, associated with geographical location, involved populations of *obesus* east of eastern Alberta, of *brevicomis* from California to British Columbia, of *frontalis* from the United States, and of *murrayanae* from the western United States.

In *obesus* there was a greater tendency for fully mature (senile?) specimens to turn black with age in the western part of its range. Since this also occurs with *Trypodendron lineatum* (Wood, 1957:340), and possibly with other bicolored scolytid species, it may be caused by ecological factors. The frons of *obesus* also tended to be more densely granulate in western specimens, however, this character affected less than half of any series examined.

The frons varied conspicuously in *frontalis* from locality to locality. Almost every local population exhibited its own frontal characters which were consistent within that population. It was of interest, however, that one extreme variation in a series from Prescott, Arizona, also appeared in a West Virginia series.

The size of punctures on the pronotal disc varied tremendously between individuals of almost any local population, but variations apparently dependent on geographical origin were detected in two species. In *ponderosae* from central or southern California the pronotal disc commonly was uniformly, minutely punctured. These specimens always occurred with specimens tending to be more coars-

ely punctured. This character gradually faded from the population toward northern California. This variation was not associated with Jeffrey pine or any other host, as reported by Hopkins (1909). A somewhat similar variation in *murrayanae* probably occurs, but too few specimens were available to consider it fully.

Geographical variation in *brevicomis* involving the sculpture of the elytra was reported by Hopkins (1909). While his observations tend to be correct, it was observed that the most coarsely sculptured individual specimens of this species examined during this study came from northern California; the most finely sculptured came from western Chihuahua. Since this character cannot be measured with accuracy, and since definite patterns in the distribution could not be established using this character, it could not be employed to characterize geographical races. Somewhat similar variations were reported by Hopkins (1909) in *parallelocollis*, but may be attributed to the inadequacy of series available for study at that time.

Phylogeny

In treating the relationships of *Dendroctonus* to other genera of Scolytidae it is apparent that certain morphological and biological characters exist that might be useful in analyzing the lines of specialization observed within this genus. For example, only the most closely related of the genera allied to *Dendroctonus* have an evident epistomal process; elaborations of this structure within the genus would, then, appear to represent specialization of this character, and the absence of special modifications would appear to represent a primitive condition. Frontal grooves and tubercles and the specialized transverse callus of the pronotum are absent in allied genera, as well as in most species of *Dendroctonus;* therefore, their presence in *brevicomis*, *frontalis*, *parallelocollis* and *adjunctus* (groove only) evidently represents specialization. These four species also share the habits of constructing sinuate egg galleries and of placing their eggs in individual egg niches alternately on the sides of the gallery. The sinuate gallery is a departure from the typical straight, vertical hylesinine gallery, but the alternate placement of eggs definitely is primitive.

Among the largest species of the genus, increased size appears to be a departure from allied genera, hence is a specialization. Another specialization appears to be the reduction in size of the strial punctures on the declivity. In *pseudotsugae* and *simplex* extension of the epistomal process toward the epistomal margin and the deeper second declivital interspace are departures exhibiting specialization. The most striking specializations among the larger species, however, are biological; of special importance are the methods of egg deposition and of larval excavation. In all of these species the egg galleries basically are straight. Eggs are deposited in individual niches in *ponderosae* with niches placed in groups of one to eight first on one side of the gallery and then on the other. In the remaining

species eggs are deposited in grooves along the sides of the egg gallery in batches of one to several dozen. In *pseudotsugae* and possibly *simplex* (not observed) each egg is oriented in a definite way; in the remaining species they are deposited at random without orientation. The larvae of *pseudotsugae* and *simplex* construct individual mines that seldom cross one another. In the remaining species observed during this study that share this method of egg deposition, the larvae feed in congress. This communal feeding continues in *obesus* until about the second instar when each larva constructs an individual mine that may cross and recross those of other larvae. In *valens* and *terebrans* communal feeding usually continues until pupation. In *murrayanae* groups of second instar larvae separate from one another, but reunite later into a common chamber. It is presumed that *micans* and *punctatus* share this latter habit, although neither was observed during this study.

When all morphological characters are considered *aztecus* undoubtedly is the most primitive species in the genus. The epistomal process, frons, prothorax, elytral declivity and absence of sexual differences match rather closely those of the hypothetical ancestor of the genus. It also bears a deceptive resemblance to *Hylurgus* or *Tomicus*. Unfortunately, the biology of *aztecus* was not studied in sufficient detail for use in a consideration of phylogeny.

On the basis of this study the following groups of closely allied species occur in the genus; they are listed in the order of increasing specialization, although the evolutionary relationships among the groups is uncertain.

1. *frontalis*, *brevicomis*, *parallelocollis*.
2. *aztecus*, *valens*, *terebrans*.
3. *adjunctus*, *ponderosae*.
4. *obesus*, *murrayanae*, *punctatus*, *micans*.
5. *simplex*, *pseudotsugae*.

It is clearly evident that *frontalis* and *brevicomis*, *valens* and *terebrans*, *murrayanae*, *punctatus* and *micans*, and *simplex* and *pseudotsugae* are geographical replacements of one another that developed in comparatively recent geological time. With the exception of *micans*, however, their distributions now overlap in some parts thereby removing all doubts concerning their specific identities. Although much more remote, it is also evident that *parallelocollis* arose in a similar manner from common ancestry with *frontalis-brevicomis*, *ponderosae* from *adjunctus* ancestry, and *obesus* from *murrayanae-punctatus-micans* ancestry. The structural bases for these conclusions are included in the key to species, and in the treatment of the various species.

Genus *DENDROCTONUS* Erichson

Dendroctonus Erichson, 1836, Archiv f. Naturgesch. 2(1):52; Ratzeburg, 1837, Die Forstinseketen, p. 217; Eichhoff, 1864, Berliner Ent. Zeitschr. 8:26;

Lacordaire, 1866, Genera des Coléoptères 7:360; Zimmerman, 1868, Tans. American Ent. Soc. 2:148; Leconte, 1868, Trans. American Ent. Soc. 2:172; Chapuis, 1869, Synopsis des Scolytides, p. 34 (1873, Mém. Soc. Roy. Sci. Liége (2)3:242); Leconte, 1876, Proc. American Philos. Soc. 15:384; Provancher, 1877, Fauna Ent. Canada 1:572; Lindeman, 1879, Bull. Soc. Imp. Nat. Moscou 54:53; Eichhoff, 1880 (1881), Die Europäischen Borkenkäfer, p. 125; Leconte and Horn, 1883, Coleoptera of North America, p. 523, Reitter, 1884, Verh. naturf. Ver. Brünn 33:53; Dietz, 1890, Trans. American Ent. Soc. 17:27; Blandford, 1897, Biol. Centr.-Amer., Coleoptera 4(6):146; Lovendal, 1898, De Danske Barkbiller, p. 86; Hopkins, 1899, West Virginia Agric. Expt. Sta. Bull. 56:392; Barbey, 1901, Scolytides l'Europe Central, p. 55; Hopkins, 1902, Proc. Ent. Soc. Washington 5(1):3; Formánek, 1907, Kurovici v Cechach a na Morave zyící, p. 21; Swaine, 1909, New York St. Mus. Bull. 134:95; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):1-64 (monograph); Hagedorn, 1910, Coleopterorum Catalogus 4:19; Hagedorn, 1910, Genera Insectorum 111:59; Reitter, 1913, Wiener Ent. Zeit. 32(Behheft):47; Saalas, 1914, Medd. F. et Fl. Fenn. 40:77; Hopkins, 1914, Proc. U. S. Natl. Mus. 48(2066):120; Hopkins, 1915, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(2):168; Blatchley and Leng, 1916, Rhyncophora or weevils of N. E. America, p. 652; Swaine, 1918, Dom. Canada Dept. Agric. Ent. Br. Bull. 14(2):60; Leng, 1920, Cat. Coleopt. America north of Mexico, p. 338; Blackman, 1922, Mississippi Agric. Expt. Sta. Tech. Bull. 11:56; Spessivtseff, 1925, Svensk Insektfauna 3:164; Spessivtseff, 1931, Opredelitel Korojedov, p. 86; Schedl, 1932, *in* Winkler, Cat. Coleopt. reg. palaearcticae, p. 1635; Dodge, 1938, Univ. Minnesota Agric. Expt. Sta. Tech. Bull. 132:26; Chamberlin, 1939, Bark and timber beetles of North America, p. 144; Schedl, 1940 (1939), Ann. Esc. Nac. Cienc. Biol. (Mexico) 1:339; Blackwelder, 1947, U. S. Natl. Mus. Bull. 185:784; Balachowsky, 1949, Faune de France 50:134; Stark, 1952, Fauna U.S.S.R. 33:184; Schedl, 1955, Zeitschr, angew. Ent. 38:7; Pfeffer, 1955, Fauna C.S.R. (Czechoslovakia), p. 121; Chamberlin, 1958, Scolytoidea of the Northwest, p. 64. BIOL.: Smith, 1877, Shade trees . . . and Insects that infest them, p. 52; Cockerell, 1893, Trans. American Ent. Soc. 20:336; Judeich-Nitsche, 1895, Forstinsekten 1:445; Chittenden, 1899, U. S. Dept. Agric. Div. For. Ent. Bull. 18(5):55; Felt, 1906, New York St. Mus., Mem. 8, 2:337; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 83(1):169; Herrick, 1910, Rur. New York, p. 896; Yates, 1910, Engineer News, p. 517; Craighead, 1928, Jour. For. 26(7):886; Inda, 1930, Mexico Forest. 8(8):173; Keen, 1938, U. S. Dept. Agric. Misc. Pub. 273:98; Shull, 1944, Idaho Expt. Bull. 252:5; Keen, 1949, U. S. Dept. Agric. Yearbook 1948:427.

Dendroctonus is not very closely allied to any known genus, but unquestionably is related to *Hylurgus* Latreille and *Tomicus* Latreille (=*Blastophagus* Eichhoff) of Europe and Asia, to *Pachycotes* Sharp of Australia and New Zealand, and to *Hylurgonotus* Schedl of South America. It differs from these genera, however, by the well developed, unique epistomal process (very poorly, narrowly indicated in *Hylurgonotus brunneus* Schedl and in *Pachycotes*), by the five-segmented antennal funicle, by the absence of a broad impression on the frons of the male (very feebly indicated in *Tomicus*), and by the strongly flattened antennal club.

Description.—Length 2.5-9.0 mm., 2.3-2.6 times as long as wide; body color dark brown to black, some species with reddish brown elytra.

Frons convex, with or without secondary sexual characters expressed as elevations, tubercles, etc.; epistomal margin laterally elevated, smooth, shining; epistomal process well developd just above

elevated portion of epistomal margin, overlapping and extending almost to or flush with median portion of epistomal margin, its basal width equal to a distance one-fourth to one-half as great as distance between eyes, flat or transversely concave between its lateral margins (arms); surface varying from smooth and punctured in some species to densely granulate in others; vesiture hairlike, moderately long, fine, sparse, inconspicuous. Eye ovate, short and broad to rather long and narrow; entire; finely granulate. Antennal scape elongate, clavate; funicle five-segmented, increasing strongly in width from segment two to five, pedicle only slightly wider than two; club strongly flattened, subcircular in outline, with three weakly to strongly procurved sutures indicated only by setae.

Pronotum 1.2-1.4 times as wide as long, widest on basal third; sides feebly to moderately arcuate and more or less converging toward the broadly, shallowly emarginate anterior margin, with or without a prominent constriction just behind anterior margin; surface smooth and shining, with conspicuous, rather deep punctures of variable size more or less characteristic of each species; basal margin almost straight to bisinuate; lateral margins rounded. Vestiture hairlike, sparse to moderately abundant, short to rather long.

Elytra 2.1-2.5 times as long as pronotum; sides straight and subparallel on basal two-thirds, rather broadly rounded behind; scutellum rather small, somewhat depressed in basal notch between elytra; basal margins somewhat arcuate and bearing a row of about nine to twelve moderately large, raised, overlapping crenulations, with several smaller submarginal ones particularly on interspaces two and three; striae impressed or not, the punctures rather large and moderately deep; interstriae feebly to not at all convex, about one to two times as wide as striae, armed by variable transverse crenulations. Declivity rather steep, convex; variously sculptured. Vestiture hairlike; variable.

Type species.—*Bostrichus micans* Kugelann, subsequent designation (Hopkins, 1909:5) (cf. discussion of history above).

Key to the species of *Dendroctonus*

1. Frons with a rather deep, narrow median groove extending from just above epistomal process to upper level of eyes; if median impression obscure in male the lateral areas of frons rather strongly protubrant and usually armed by one or two tubercles (except *adjunctus*), if protubrance obscure in female then anterior constriction of pronotum with a transverse elevated callus (Figs. 5, 9) laterally and dorsally (obscure laterally in *adjunctus*); epistomal process very broad with the lateral margins prominently raised; smaller species 2.5-7.4 mm., in *Pinus* 2

   Frons without a median groove or impression below upper level of eyes; lateral elevations of frons and transverse elevated callus of pronotum never present in either sex; epis-

tomal process usually narrower and less prominent, the lateral margins raised or not; larger species 5.0-9.0 mm. (rarely as small as 3.7, or 3.4 in *simplex*), in *Pinus* and other conifers 5

2. Punctures and/or granules of second declivital interspace more abundant, confused; second declivital interspace as wide as one and three, not constricted apically (Fig. 27); smaller species, 2.5-5.0 mm. 3

Granules of second declivital interspace rather sparse and uniseriate; second declivital interspace narrower than one and three or strongly constricted apically (Fig. 30); larger species, 3.8-7.4 mm. 4

3. Declivital pubescence rather abundant and uniformly short, not longer than a distance equal to half the width of an interspace; transverse discal rugae on posterior half of discal interspaces almost never longer than half the width of an interspace; declivital striae usually not impressed, obscure; punctures of declivital interspaces more abundant and feebly if at all granulate (Fig. 27). ..... *brevicomis* Leconte

Declivital pubescence less abundant, at least some hairs twice as long as width of an interspace; at least a few rugae on posterior half of elytral disc as wide as the interspace; declivital striae usually impressed, the punctures larger and distinct from those of interspaces; punctures of declivital interspaces less abundant and more coarsely granulate (Fig. 28) ..... *frontalis* Zimmerman

4. Granules on declivital interspaces one and (usually) three more abundant, confused; transverse elevation of female pronotum very prominent laterally; male frons with prominent lateral tubercles (Figs. 7-10); larger, 4.5-7.4 mm.; stouter, 2.5 times as long as wide ..... *parallelocollis* Chapuis

Granules on declivital interspaces one and three sparse, uniseriate; transverse callus of female pronotum obscure laterally; male frons without lateral tubercles (Figs. 11-12); smaller 3.8-6.0 mm.; more slender, 2.65 times as long as wide ..... *adjunctus* Blandford

5. Declivital interspaces dull (minutely rugulose) or shining, if shining the punctures virtually all granulate in both sexes and strial punctures distinct and larger; epistomal process rather broad, the distance between eyes not more than 2.2 times its basal width; episternal area of prothorax more coarsely granulate, the punctures obscure or absent 6

Declivital interspaces smooth and shining, most of the punctures impressed, a few of them granulate in female; epistomal process rather narrow, the distance between eyes

three or more times its basal width; episternal area of prothorax punctate, the granules minute or entirely absent 9

6. Surface of declivity opaque (usually rugulose); second declivital interspace impressed, usually flat, interspace one strongly and three weakly elevated; declivital interspaces usually uniseriately granulate and with scattered fine punctures ..... *ponderosae* Hopkins

Surface of declivity usually shining, the second interspace not impressed and sutural interspace weakly if at all elevated; virtually all of the rather numerous punctures on declivital interspaces granulate, the granules close, confused 7

7. Epistomal process broad, flat, the margins not elevated (Fig. 24); strial punctures rather small and obscure, rugae of discal interspaces very coarse, many as wide as interspace, a few crossing striae; frons strongly evenly convex; pronotum gradually narrowed anteriorly, without an abrupt constriction (Figs. 25-26) ..... *aztecus*, new species

Epistomal process broad, transversely concave, the margins strongly elevated (Figs. 14-16); strial punctures larger, never traversed by the smaller discal rugae; frons irregularly less strongly convex; pronotum feebly if at all narrowed anteriorly, with an abrupt constriction just behind anterior margin (Fig. 17) 8

8. Body color of mature specimens black; punctures on disc of pronotum rather coarse, those near lateral margin much larger; declivital tubercles usually larger, apparently more numerous (Fig. 29); southeastern United States ..... *terebrans* (Olivier)

Body color of mature specimens reddish brown; punctures of pronotum not as coarse, those near lateral margin similar to those on disc; declivital tubercles usually smaller, apparently less numerous (Fig. 30); North America, except southeastern United States ..... *valens* Leconte

9. Declivital striae weakly if at all impressed, the second apically curved toward sutural striae; declivital interspace one feebly elevated, two as wide or wider than one or three (except near apex); discal striae less than half as wide as interstriae; epistomal process usually transversely concave (except *micans*), rather broad, the lateral margins moderately oblique (less than 55° from the horizontal) (Figs. 18-21) 10

Declivital striae strongly impressed, the second straight; declivital interspace one strongly elevated, two weakly impressed and narrower than one and three; discal striae almost as wide as interstriae; epistomal process flat or convex, narrow, the lateral margins strongly oblique (about 80° from

the horizontal) (Figs. 22-23) 13

10. Frons smooth and polished, with deep close punctures, but almost entirely without granules between punctures (Figs. 18, 21); strial punctures on declivity rather large, three or more times as large as those of interstriae 11

Frons rather finely granulate between the close, deep punctures (granules sometimes obscure in *murrayanae*) (Figs. 19-20); strial punctures on declivity usually minute, seldom more than twice as large as those of interstriae 12

11. Epistomal process flat; stouter, 2.3 times as long as wide; strial punctures more strongly impressed; larger, 6.0-8.0 mm.; northern Europe and Asia ..... *micans* Kugelann

Epistomal process shallowly, transversely concave; more slender, 2.4 times as long as wide; strial punctures shallowly impressed; smaller, 5.4-6.5 mm.; northeastern North America to Alaska, in *Picea* ..... *punctatus* Leconte

12. Frons coarsely, distinctly punctured, the granules between them usually isolated from one another, often very sparse (Fig. 19); male genitalia as figured (Fig. 39); from *Pinus* ..... *murrayanae* Hopkins

Frons very closely, more coarsely granulate, the punctures usually obscure in central area (Fig. 20); male genitalia as figured (Fig. 40); from *Picea* ..... *obesus* (Mannerheim)

13. Frons moderately protubrant, smooth with rather coarse, deep punctures (Fig. 22); punctures of pronotum rather large; discal interstriae with fine punctures interspersed with small rugae; smaller, 3.4-5.0 mm.; eastern North America to Alaska; from *Larix* ..... *simplex* Leconte

Frons strongly protubrant, irregular, granulate, with rather fine, deep punctures (Fig. 23); punctures of pronotum rather small; discal interstriae without fine punctures dispersed among rugae; larger, 4.4-7.0 mm.; western North America; from *Pseudotsuga* and *Larix* ..... *pseudotsugae* Hopkins

Dendroctonus brevicomis Leconte

Figs. 1-2, 27, 31-32, 43-46.

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This species is very closely related to *frontalis*, but is readily distinguished by the uniformly short declivital pubescence, by the less strongly impressed declivital striae, by the more numerous, more finely granulate punctures of the declivital interspaces, by the larger average size, and, in part, by the distribution.

Male.—Length 2.5-5.0 mm. (average about 4), 2.4 times as long as wide; mature color very dark brown.

Frons convex, with a pair of lateral elevations on median half just below upper level of eyes separated by a deep median groove, the summits of elevations armed at their dorsomedian margins by one or two prominent, somewhat dorsomedially oriented granules; epistomal margin elevated, its surface smooth and shining; epistomal process half (0.50 times) as wide as distance between eyes, its arms oblique (about 40° from the horizontal) and elevated, the horizontal portion about half its total width, transversely concave, overlapping and ending just above epistomal margin and bearing under its distal margin a dense brush of conspicuous yellowish setae; surface punctate-rugulose above eyes, more deeply punctured and subgranulate below. Vestiture, except epistomal brush, short, sparse, inconspicuous.

Pronotum 1.4 times as wide as long, widest on basal third; sides rather strongly arcuate on basal three-fourths, rather strongly constricted just behind the broadly, shallowly emarginate anterior margin; surface smooth with rather fine, shallow, close punctures on median third, becoming more finely punctured laterally; an indistinct median line apparent. Vestiture very short, rather sparse, inconspicuous.

Elytra 2.2 times as long as pronotum; sides straight and subparallel on basal two-thirds, rather broadly rounded behind; basal

margins arcuate and bearing a row of about nine moderately large, raised, overlapping crenulations, with several smaller submarginal ones particularly on interspaces two and three; striae weakly impressed, the punctures rather small and shallow; interstriae about twice as wide as striae and armed by abundant, confused, small, transverse crenulations, each averaging about one-third the width of an interspace, never more than half as wide on posterior half of disc. Declivity moderately steep, convex with a feeble impression between first and third striae; strial punctures reduced in size; interstrial punctures ranging from finely granulate to not at all granulate, abundant, confused (about three to four irregular ranks across width of an interspace). Vestiture rather abundant, short, averaging about half as long as width of an interspace, never as long as its entire width.

Female.—Similar to male except lateral elevations of frons less prominent and unarmed, with median groove consequently less conspicuous; arms of epistomal process less strongly elevated; pronotal constriction largely filled by a prominent transverse elevated callus both laterally and dorsally; punctures of pronotal disc very slightly larger and deeper; transverse crenulations of elytral disc very slightly larger; and declivital granules much finer, only a few punctures with a minute granule on upper margins.

Type locality.—Middle California (Williams, Arizona, for *barberi*). The types of both descriptions were examined.

Hosts.—*Pinus ponderosa*, and *P. coulteri*. Rarely, particularly during epidemics, other species of *Pinus* may be attacked.

Distribution.—North America west of the Rocky Mountains from Chihuahua to British Columbia wherever the principal host tree, *Pinus ponderosa*, occurs.

Specimens from the following localities were examined (Fig. 45). ARIZONA: Carr Canyon, Chiricahua Mts., Coconino N. F., Crow King, "Deadmans Flat" (Coconino Co.), Flagstaff, Ft. Apache, "Fort Valley," Grand Canyon N. P., Groom Ck. (Prescott N. F.), Huachuca Mts., "Pleasant Valley," Prescott, San Francisco Mts., Santa Catalina Mts., Santa Rita Mts., Springerville, Walnut Canyon N. M., Williams, "Willow Rock," and Young. CALIFORNIA: Alta, "Atwell's Mill," Badger, Ballard, "Barton Flat" (San Bernardino N. F.), Bass Lake, "Battle Creek R. S." (Shasta Co.), "Bear Flat" (Warner Mt.), Berkeley, "Better Waller R. S.," Black's Mt., Blue Canyon, Blut Mt., Bray, Breckenridge Mt., "Buck Ck.," Burney, "Butte Ck. Basin" (Butte Co.), "Campbell Hot Springs," "Capanero Ck.," Carrville, Castella, Cayton, Cecilville, Cedar Grove (Kings Can. N. P.), "Cedar Ridge" (Glenn Co.), Chester, Cisco, "Clairsville," Coarsegold, Corte Madera, Crane Valley, "Cummings R. S. (Eldorado Co.), Cuyamaca Rancho St. P., Crystal Lake, "D. & H. Mill" (Madera Co.), Deep Creek, Diamond Springs, "Dixie Valley" (Lassen Co.), Dunlap, Elk Creek, "Figueroa Mt.," Fish Camp, Foresthill, Giant Forest, Hackamore, Happy Camp, "Harvey Valley" (Alameda Co.), Hayfork, "Hazel Green," Hobergs, Hot Springs, Idyllwild, Jackson Ck., Julian, "Kangaroo R. S.," Kaweah, Kaweah River, Kelsey, Kings Canyon, Klamath N. F., Kyburz, "Lagunas," Lake Almanor, Lake Arrowhead, "Little Humbug R. S.," "Little Yosemite," Long Barn, Lookout, Los Olivos, "Lumgray R. S.," Mather, McCloud, McLears Resort (Plumas Co.), Meadow Valley, Miami R. S., Milford, "Millwood," Miramonte, Modoc N. F., "Madrone Spring," Moffit Ck., "Mosquito," Mt. Hermon, "Nash Mine"

Fig. 45. Probable geographical distribution of *Dendroctonus spp.* with collection sites indicated: 1, *brevicomis* (circles); 2, *frontalis* (triangles).

(Trinity Co.), "Nigger Spring" (Lassen Co.), North Fork, N. Fk. Eel River, "Norton's Mill (Siskiyou Co.), "Norvell Flats" (Lassen Co.), "Oak Flat Camp" (Fresno Co.), "Onion Valley," Placerville, Plumas N. F., Pinecrest, Pinehurst, Pine Valley, "Pinoche R. S." (Mariposa Co.), Prattville, "Quintette," Santa Cruz, Shasta Springs, Sisson, Stirling City, Sugar Pine, "Summerdale," "Summit Lake" (Shasta Co.), Tenaya Lake, Three Rivers, Timber Mt., Tuolomne Meadows, Wawona, "Whitehall," White Hills, Willow Ranch, Wishon, Yosemite N. P., and Yreka. COLORADO: Dolores, Ft. Garland, "Vallecito R. S." (La Plata Co.), Monte Vista, and Uncompahgre N. F. IDAHO: Boise, Cedar Mt., Centerville, Couer d'Alene, Garden Valley, Kooskia, Moscow, Pioneer, Placerville, Smith's Ferry, Stites, and Troy. MONTANA: Missoula. NEVADA: Las Vegas. NEW MEXICO: Capitan Mts., Cloudcroft, Datil, Gloriela Mesa, Mescalero, Mimbres, Ruidoso, Santa Fe, Santa Catalina Mts., Zuni Mts., and Jermejo Park. OREGON: Ashland, Bend, Blue Mts., Bly, Burnt River, Chiloquin, Cold Springs, Colestin, Corvallis, "Dutch Ck.," Fremont N. F., Ft. Rock, Grants Pass, Jenny Ck., Joseph, Keno, Klamath Falls, Klamath Indian Res., Prineville, "Pringle Falls," Siskiyou Mts., Sisters, Sumpter, and Wallowa Mts. TEXAS: Big Bend and Davis Mts. UTAH: Daves Hollow (Dixie N. F.), Escalante, Panguitch, Pin Hollow (Fish Lake N.F.), and Ashley N. F. WASHINGTON: Blue Mts., Buckeye, Chelan, Dayton, Kooskooskie, Northport, Pullman, and Toppenish. BRITISH COLUMBIA: Aspen Grove, Little Shuswap Lake, "Midday Ck." in Indian Meadow, Midday Valley, "Spious Ck." Summerland, "Trepan Ck.," and "Trepanier Ck." CHIHUAHUA Tres Rios.

Geographical variation.—Specimens from the eastern parts of the range of this species, Arizona, Utah and Colorado, tend to average slightly larger in size (less than 1 mm. larger); the elytral

striae tend to be somewhat more deeply impressed; and the elytral crenulations tend to average slightly larger. These differences, however, are not sufficiently consistent in a long series from any particular locality to permit the recognition of distinct geographic races as was done previously by Hopkins (1909:70). It is of interest to note that the smallest, most coarsely sculptured specimens came from northern California; the most finely sculptured specimens, from Chihuahua, had rather strongly impressed striae (equal to specimens from any other locality); and numerous specimens, particularly females, from Utah and Arizona cannot be distinguished from the average West Coast series. The Chihuahua series, particularly, exhibited every degree of morphological intergradation between extreme eastern and western populations.

Biology.—This species probably has destroyed more merchantable timber in North America than any other organism in historic time. Estimates indicate that approximately two billion board feet of standing timber have been destroyed annually since studies commenced over half a century ago.

Overwintering parent adults and brood may become active at any period when subcortical temperatures become sufficiently high, probably somewhere in the vicinity of 45° to 50° F. The dates at which favorable conditions for flight occur in the spring vary considerably from year to year and from locality to locality depending on exposure, altitude, latitude, weather, and other ecological factors. In general the first of the overwintering adults and brood emerge to attack new trees about the first of May. Attacks from these beetles ordinarily continue until the latter part of June. A paricularly early or late season, or a change in latitude north or south of the center of distribution may alter these dates by as much as a month. In the extreme southern limits of distribution it is possible that some flight activity may continue throughout the year. Because beetles do not emerge simultaneously, but do so slowly over a considerable period of time, and because of overlapping broods some flight activity continues throughout the summer season with periods of greatest flight activity coinciding with the emergence of each new brood. Flight activity is discontinued in October or November when daytime temperatures fall below 50°.

Trees selected for attack usually are living, standing and larger than 12 inches D.B.H. Prostrate trees are seldom attacked. In the absence of competing species the attack normally is distributed from the ground level upward to areas as small as four to eight inches in diameter where cork plates of the bark have formed. Younger bark of limbs or upper bole and of smaller trees where cork plates have not developed are rarely attacked. In the presence of competing species of *Dendroctonus*, particularly *adjunctus*, and to a lesser extent *ponderosae*, the area of attack by *brevicomis* is forced upward from the ground level a variable distance depending on the comparative abundance of competing species.

The attack usually begins in the upper midbole area of the host

tree then progresses upward and downward. The attack is slow and continuous, without any sudden or concerted swarming of the beetles. Its duration is variable, evidently depending upon the population density of beetles in the area, upon resistance of the host, or upon climatic or other ecological factors peculiar to the season or locality. It may be completed in as little as seven days, or it may continue over the greater part of a year. Characteristically the attack will be concentrated on one particular tree until it is overcome, even when the beetle population is high, before an attack is started on a second nearby tree. There is no attempt to occupy all available bark; the density of individual attacks may be as low as an average of about five per square foot of suitable bark on a susceptible tree, or higher than 20 per square foot on a vigorous or resistant tree. In general, single tree attacks suggest an endemic condition, while group attacks suggest an epidemic condition.

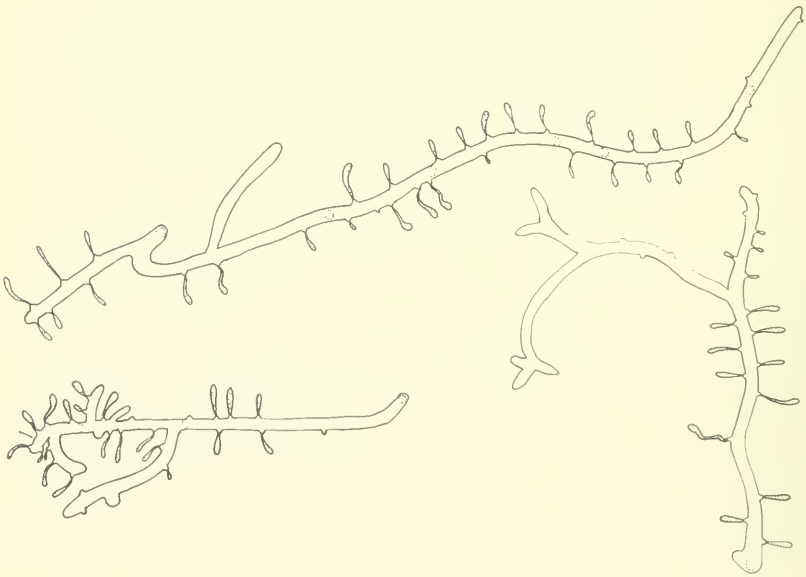

Fig. 46. *Dendroctonus brevicomis*: Egg galleries sinuate, predominantly transverse; egg niches large, placed individually on alternate sides of gallery; larval mines turn into outer bark and expand after a brief contact with the cambium.

The winding egg galleries (Figs. 43, 46) are constructed almost entirely in the inner bark or phloem tissues; they are in continual contact with and very lightly score or stain the woody or xylem tissues. Their total lateral displacement usually is equal to or greater than the total longitudinal displacement, although an occasional gallery may be decidedly longitudinal.

The diameter of an individual egg gallery is slightly greater than the width of a beetle; it averages approximately 35 cm. in

length, although exact measurements of fully formed galleries are virtually impossible to obtain because of the tendency for the winding galleries to branch, to anastomose, and to cross and recross one another. It is not uncommon for more than one pair of beetles to occupy one gallery, usually each pair being found in different branches that use the same entrance hole. Presumably this habit has suggested a tendency toward polygamy to some workers, particularly when the male was late in arriving or failed to arrive at all.

The initial attack is made by the female, usually in a crevice of the bark. About the time she reaches the phloem tissues where the pitch begins to flow she is joined by the male who then assists her by pushing the excavated frass out of the entrance hole. Continuation of the parental or egg gallery is performed entirely by the female beetle. After several inches of gallery have been cleared and the frass ejected from the entrance hole, the male then packs the frass in the lower regions of the gallery thereby closing the entrance hole and tightly filling the gallery except for a few inches in the area where the beetles are working. It has been estimated that (Miller and Keen, 1960:16) about two-thirds of an inch of new gallery is formed each day. Mating occurs only after the female has been joined by the male, never on the surface of the tree before the attack begins. Although seldom seen, mating evidently occurs repeatedly, since it has been observed in various stages of gallery construction.

Ordinarily, but not always, the entrance tunnel is without a nuptial chamber or other means of turning around until the first ventilation tunnel or branch in the gallery is reached. Ventilation tunnels (indicated by dotted circles in Fig. 46) are placed at irregular intervals and are not always present. Their presence appears related to the stage of gallery construction, thickness of the bark, and activity of the beetles. Usually they are not constructed before the entrance hole is plugged by frass; they are less abundant or sometimes entirely absent in trees having comparatively thin bark; and they appear to be more numerous in galleries constructed by unusually active beetles. Seldom are they spaced at intervals less than five centimeters.

Oviposition ordinarily begins about eight days after the attack and continues for approximately 10 to 49 days (Miller and Keen, 1960:20), except when egg-laying is interrupted by winter in which case it is greatly extended. Although estimates of the number of eggs produced by a female based on the average number of eggs per inch of gallery have suggested a figure much higher, the highest number actually reported is 41 (Miller and Keen, 1960:19). Usually a majority of the eggs are deposited in the first third of the gallery, the number declining significantly in the final third.

Egg niches are symmetrical and ordinarily are constructed on the sides of the gallery, usually in direct contact with the cambium. They are broad and deep, the depth being equal to about one-fourth

to one-third the diameter of the egg gallery. The deepest point is rounded, matching rather well the anterior profile of the parent beetle as seen from the dorsal aspect. Unfilled egg niches often cannot be distinguished from the beginning of a new branch of the gallery. The number and spacing of niches depends on many factors, but usually the minimum distance between eggs on a particular side of a gallery is one centimeter. When considering both sides of the gallery and the alternating placement of eggs this distance is reduced by half. Eggs are deposited individually in the niches; each niche is then filled by specially prepared frass packed to the original level or contour of the gallery.

Following the period of oviposition the gallery may be continued in an irregular feeding tunnel of somewhat greater diameter than usual until death of the parent bettle, or the beetles may construct an exit tunnel, often independent of one another, by extending one of the ventilation tunnels and emerge to attack another host tree. It has been estimated that as many as 50 percent of the parent beetles emerge to produce a second brood, and a few of these re-emerge to produce their third brood of the season (Miller and Keen, 1960:18). Of those beetles that re-emerge from the host males predominate significantly.

The incubation period has not been determined precisely. Available figures suggest that seven days are required for hatching under optimum conditions (Miller and Keen, 1960:20), presumably with longer periods required when less favorable conditions exist. The newly-hatched larvae mine the phloem next to the cambium for approximately one centimeter at right angles to the egg gallery. They then move into the inner bark and end their tunnels near the outer bark where an area is cleared for pupation. Under optimum conditions larval development may be completed in as little as 30 to 35 days (Miller and Keen, 1960:24); however, they do not develop at the same rate and some may require as much as 300 days to complete the larval stage of development. In the pupation cell the larva undergoes physiological changes to become a quiescent prepupa for about two to seven days before pupation occurs (Miller and Keen, 1960:30); mature larvae overwinter as prepupae, never as pupae. Under normal conditions about 6 to 20 days are required to complete the pupal stage (Miller and Keen, 1960:31), unfavorable conditions may extend this period. A maturation period between attainment of the adult stage and emergence from the host varies from 7 to 14 days (Miller and Keen, 1960:31), except in the spring months when it may be somewhat longer.

The number of generations each year is complicated by peculiarities of a particular season, by re-emergence of parent adults to produce a second or a third brood, and by overlapping generations. In the northern parts of its range one complete and a partial second generation appears normal, in southern California and in Arizona three complete and perhaps a partial fourth generation might be expected.

Dendroctonus frontalis Zimmerman

Figs. 3-6, 28, 33, 45, 47.

Dendroctonus frontalis Zimmerman, 1868, Trans. American Ent. Soc. 2:149; Leconte, 1868, Trans. American Ent. Soc. 2:173; Leconte, 1876, Proc. American Philos. Soc. 15:386; Dietz, 1890, Trans American Ent. Soc. 17:32 (part); Hopkins, 1902, Proc. Ent. Soc. Washington 5:3; Swaine, 1909, New York St. Mus. Bull. 134:96; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):90; Hagedorn, 1910, Coleopterorum Catalogus 4:20; Hagedorn, 1910, Genera Insectorum 111:60; Hopkins, 1915, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(2):211; Blatchley and Leng, 1916, Rhynchophora or weevils of North Eastern America, p. 653; Chamberlin, 1939, Bark and Timber Beetles of North America, p. 165. BIOL.: Packard, 1890, U. S. Ent. Comm. Rept. 5:722; Hopkins, 1892, Poc. Ent. Soc. Washington 2:353; Hopkins, 1892, Science, July 29, 20:64; Hopkins, 1893, West Virginia Agric. Expt. Sta. Bull. 31:143, 32:213; Hopkins, 1893, Insect Life 5:187; Riley, 1893, Insect Life 6:140; Hopkins, 1893, Insect Life 6:126; Hopkins, 1894, Canadian Ent. 26:280; Lintner, 1894, Gardening 2:292; Hopkins, 1896, Canadian Ent. 28:250; Chittenden, 1897, U. S. Dept. Agric. Div. Ent. n. s., Bull. 7:67; Schwarz, 1898, Proc. Ent. Soc. Washington 4:81; Hopkins, 1898, Proc. Soc. Prom. Agric. Sci. 19:103; Hopkins, 1899, West Virginia Agric. Expt. Sta. Bull. 56:395; Hopkins, 1899, Proc. Ent. Soc. Washington 4:343; Hopkins, 1899, U. S. Dept. Agric. Div. Ent. Bull. 21:13, 14, 27; Lugger, 1899, Minnesota Agric. Expt. Sta. Bull. 66:315; Chittenden, 1899, U. S. Dept. Agric. Div. Foestry Bull. 22:55; Hopkins, 1901, U. S. Dept. Agric. Div. Ent. Bull. 28:pl. XII.; Hopkins, 1902, U. S. Dept. Agric. Div. Ent., n. s, Bull. 37:20; Hopkins, 1903, U. S. Dept. Agric. Yearbook 1902:270; Hopkins, 1903, Canadian Ent. 35:59; Hopkins, 1904, U. S. Dept. Agric. Div. Ent. Bull. 48:41, 44; Hopkins, 1904, U. S. Dept. Agric. Yearbook 1904:270; Hopkins, 1905 (1906), Proc. Ent. Soc. Washington 7:80; Currie, 1905, U. S. Dept. Agric. Div. Ent. Bull. 53:100; Felt, 1905, New York St. Mus., Mem., 8, 1:6; Webb, 1906, U. S. Dept. Agric. Yearbook 1905:632; Webb, 1906, U. S. Dept. Agric. Yearbook 1906:515; Zavitz, 1906, Ontario Ent. Soc. Rept. 36:126; Howard, 1906, U. S. Dept. Agric. Div. Ent. Rept. 1906:14; Hopkins, 1908, U. S. Dept. Agric. Yearbook 1907:163; Zavitz, 1908, U. S. Dept. Agric. Yearbook 1907:549; Fiske, 1908, Proc. Ent. Soc. Washington 9:24; Hopkins, 1908, Proc. Ent. Soc. Washington 9.131; Zavitz, 1909, U. S. Dept. Agric. Yearbook 1908:574; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 58:58; Hopkins, 1909, U. S. Dept. Agic. Bur. Ent. Bull. 83:56; Hopkins, 1910, U. S. Dept. Agric. Bur. Ent. Circ. 125:1; Hopkins, 1911, St. Louis Lumberman, July 1, p. 669; Hopkins, 1911, U. S. Dept. Agric. Farmers Bull. 476, 15 p.; Mason, 1911, South. Lumberman, Sept. 30, p. 35; Hinds, 1912, Alabama Poly. Circ. 15; Mattoon, 1915, U. S. Dept. Agric. Bull. 244:35: Murphy, 1917, U. S. Dept. Agric. Bull. 544:27; Hopkins, 1919, American Lumberm. 2299:43; Hopkins, 1919, Sci. Month. 8:503; Boving and Champlain, 1921, Proc. U. S. Natl. Mus. 57:575; Hopkins, 1921, U. S. Dept. Agric, Farmers Bull. 1188, 15 p.; Blackman, 1922, Mississippi Agric. Expt. Sta. Tech. Bull. 11:58; Berckes, 1924, American Lumberm. 2554:80; Berckes, 1924, Lumberman 73(1025):10; Felt, 1924, Manual of Tree and Shrub Insects, p. 252; Howard, 1924, U. S. Dept. Agric. Bur. Ent. Rept. 1924:26; Middleton, 1924, U. S. Golf Assoc. Green Sec. Bull. 4:148; St. George, 1924, Lumber Trade Jour. 86(9):37; St. George, 1924, Proc. South. Logging Assoc. 14:79; Wyman, 1924, U. S. Dept. Agric. Forest Serv. Bull. 8(40):2; Anonymous, 1924, Natl. Lumberman 73:10; Craighead, 1925, Jour. Forestry 23:349; Craighead, 1925, Jour. Econ. Ent. 18:557; St. George, 1952, American Lumberm. 2607:50; Schoene, 1926, Virginia St. Crop Pest Comm. Quar. Bull. 7:4, 23; Beal, 1927, Jour. Forestry 25:741; Craighead, 1927, U. S. Dept. Agric. Circ. 411:9; Craighead, 1928, Jour. Foresty 26:886; Craighead and St. George, 1928, Forest Worker 4(2):11; St. George, 1928, Forest Worker 4(5):15; Nelson and Beal, 1929,

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Dendroctonus mexicanus Hopkins, 1905 (1906), Proc. Ent. Soc. Washington 7:80 (preprint) (*new synonymy*); Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):97; Hagedorn, 1910, Coleopterorum Catalogus 4:20; Hagedorn, 1910, Genera Insectorum 111:60; Hopkins, 1915, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(2):211; Chamberlin, 1939, Bark and Timber Beetles of North America, p. 145; Schedl, 1940 (1939), An. Esc. Nac. Cienc. Biol. (Mexico) 1:339; Johnston, 1942, Proc. American Sci. Congr. (State Dept., Washington), 8:245; Muesebeck, 1950, Jour. Econ. Ent. 43:125, 131; Perry, 1951, Unasylva (Mexico) 5:159; Becker, 1951, Zeitschr. angew. Ent. 33:186; Becker, 1952, Trans. Ninth Internatl. Congr. Ent. 1:582; Becker, 1954, Zeitschr. angew. Ent. 36:20; Becker, 1955, Zeitschr. angew. Ent. 37:11; Schedl, 1955, Zeitschr. angew. Ent. 38:10. Biol.: Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 83(1):74.

This species is very closely related to *brevicomis*, but is readily distinguished by the longer declivital pubescence, by the more strongly impressed declivital striae, by the more sparsely but more coarsely granulate punctures of the declivital interspaces, by the smaller average size, and, in part, by the distribution (Fig. 45).

Male.—Length 2.3-4.5 mm. (average about 3), 2.4 times as long as wide; mature color very dark brown.

Frons convex, with a pair of lateral elevations on median half just below upper level of eyes separated by a deep median groove, the summit of elevations armed at their dorsomedian margins by one or two prominent, somewhat dorsomedially oriented granules; epistomal margin elevated, its surface smooth and shining; epis-

tomal process slightly wider than half (0.58 times) the distance between eyes, its arms oblique (about 40° from the horizontal) and elevated, the horizontal portion about half its total width, transversely concave, ending just above epistomal margin and bearing under its distal margin a dense brush of conspicuous yellowish setae; surface punctate-rugulose above eyes, coarsely, rather deeply punctured and subgranulate below. Vestiture, in addition to epistomal brush, rather long, sparse.

Pronotum 1.4 times as wide as long, widest on basal third; sides rather weakly arcuate on basal three-fourths, rather feebly constricted just behind the broadly, shallowly emarginate anterior margin; surface smooth with rather coarse, moderately deep, close punctures; punctures somewhat shallower and less abundant laterally but not reduced in size; a raised median line not apparent. Vestiture rather long, fine sparse.

Elytra 2.2 times as long as pronotum; sides straight and subparallel on basal two-thirds, rather broadly rounded behind; basal margins arcuate and bearing a row of about nine, moderately large, raised, overlapping crenulations, with several smaller submarginal ones particularly on interspaces two and three; striae rather strongly impressed, the punctures rather small, moderately deep; interstriae moderately convex, about one and one-half times as wide as striae and armed by a single very irregular row of rather coarse transverse crenulations, each averaging well over half the width of an interspace. Declivity moderately steep, convex; striae rather strongly impressed, the punctures only slightly smaller than on disc; interstriae convex, virtually all punctures rather coarsely, transversely tuberculate, arranged in an irregular single or partly double rank (never more than two ranks across an interspace). Vestiture rather abundant, rather long, length of most hairs equal to width of an interspace, a few twice as long.

Female.—Similar to male except lateral elevations of frons less prominent and unarmed, with median groove consequently less conspicuous; arms of epistomal process less strongly elevated; pronotal constrictions largely filled by a prominent transverse elevated callus both laterally and dorsally; punctures of pronotal disc very slightly larger and deeper; transverse crenulations of elytral disc very slightly larger; and declivital granules somewhat finer, a few punctures along edges of interspaces often without granules.

Type locality.—Carolina (Sacramento, Amecameca, Mexico, for *mexicanus;* Williams, Arizona, for *arizonicus*). The types of all three descriptions were studied.

Hosts.—*Pinus ayacahuite, echinata, glabra, lawsoni, leiophylla, montezumae, oocarpa, palustris, ponderosa, rigida, rudis, strobus, taeda, teocotl,* and *virginiana.* Records, presumably during epidemics, also come from *Picea excelsa,* and *rubens.*

Distribution.—North America south of a line drawn from New Jersey to central Arizona, south to Honduras.

Specimens from the following localities were examined (Fig. 45). ALABAMA: Calhoun and Montgomery. ARKANSAS: Hampton. ARIZONA: "Crook N. F.," Crown King, Flagstaff, Graham Mts., Hassayampa Lake, Jerome, Pine, "Pleasant Valley," Portal, Prescott, Prescott N. F., Rustler Park, Santa Catalina Mts., Sitgreaves N. F., Williams and Young. FLORIDA: Haw Ck., and Taylor Co. GEORGIA: Clyo, Demorest, and Thomasville. LOUISIANA: Singer, and Wilson. MARYLAND: Cumberland. NEW MEXICO: Bandelier N. M., Cloudcroft, and Mimbres. NORTH CAROLINA: Asheville, Biltmore, Black Mts., Boardman, Fletcher, "Mt. Graybeard," Pisgah Ridge, and Tryon. OKLAHOMA: "Western Indian Terr." PENNSYLVANIA: Mt. Alto. SOUTH CAROLINA: "Ben Quan," Clemson, Georgetown, and Pregnall. TENNESSEE: Ducktown. TEXAS: Beaumont, Call, Deweyville, and Kirbyville. VIRGINIA: Arlington, Auburn, Chase City, Cob Island, Glen Allen, Green Bay, King and Queen Co., Port Republic, and Virginia Beach. DISTRICT OF COLUMBIA: Washington. WEST VIRGINIA: Greenbrier, Hampshire, Hardy, Kanawha, Monongalia, Pendleton, Pocahontas, Raleigh, Randolph, Tucker, and Wood Cos. CHIAPAS: Huixtla. CHIHUAHUA: Tres Rios. DISTRITO FEDERAL: Mexico, and Tacubaya. HIDALGO: Jacala. MEXICO: Amecameca, Chapingo, San Rafael, Texcoco, and Tlalmanalco. MICHOACAN: "Michoacan." MORELOS: Cuernavaca, and Tlayacapan. PUEBLA: Texmelucan. TLAXCALA: *Tlaxcala*. ZACATECAS: Laguna Balderama. GUATEMALA: Godenez, and Santa Cruz del Quiche. HONDURAS: Olanchita, and Tegucigalpa.

Geographic variation.—Specimens from southern Mexico tend to average slightly larger in size (less than 1 mm. larger) and slightly darker in color than do those from the eastern United States. The frons varies conspicuously from area to area, but with no general trends in any direction. For example: a series from West Virginia has the frons very strongly protrubant; in series from neighboring areas the character is absent or nearly so, but reappears in a slightly modified form in one locality in central Arizona. These characters appear to characterize local populations and cannot be used to define geographic races.

Biology.—Estimates of the volume of timber destroyed annually by this insect are clouded by the difficulty of field identification in the southwestern United States and by the absence of such estimates for Mexico and Guatemala. Tremendous losses have been sustained, however, in the southeastern United States, Mexico and Guatemala which suggest the total damage resulting from activities of this insect may equal that of the Western Pine Beetle.

The winter is passed in all stages, including eggs, with larvae predominating. As with *brevicomis*, activity might resume whenever subcortical temperatures become favorable during or following the winter months. Because all stages overwinter and emerge from the host as they mature, there is an extreme overlapping of generations resulting in an almost continuous period of flight from April when the first flights of overwintering adults begin until December when activity ceases in the northern parts of the range. In southern Mexico and Guatemala it is expected that flight activity continues throughout the year without interruption. In any particular locality, however, there are periods of greatest flight activity that tend to coincide with the emergence of each new brood. According to Hopkins (1909b:62) a peculiarity of this species is its tendency to migrate considerable distances from the brood tree to begin a new at-

tack; subsequent workers (Dixon and Osgood, 1961:6) also indicate that trees selected for attack may be either nearby or considerable distances from the point of emergence.

Trees selected for attack ordinarily are living, standing and larger than about six inches D.B.H. The attack usually is concentrated on the upper half of the bole, but may reach the ground level. The attack is slow and continuous; its duration depending on numerous factors such as the size and resistance of the host, the population density of beetles in the area, the climatic and other ecological factors peculiar to the area. The duration and pattern of attack on a host tree evidently are similar to those of *brevicomis*.

The egg galleries are almost entirely in the phloem tissues, not engraving, but staining the xylem slightly. They are winding,

Fig. 47. *Dendroctonus frontalis*: Egg galleries sinuate, predominantly longitudinal; egg niches large, placed individually on alternate sides of gallery; larval mines may retain continual contact with cambium (left), or they may expand into outer bark (right).

elongate galleries (Fig. 47), often branching, anastomosing or crossing one another. The complicated interwoven series resembles rather closely that of *brevicomis*, except that there is a greater tendency for the galleries to be longitudinal; that is, for the total longitudinal displacement to exceed the total lateral displacement. The diameter of each egg gallery is slightly greater than the width of a parent beetle; in length they average approximately 30 cm., although the winding, complex character of the galleries makes accurate measurement virtually impossible.

As with other species of the genus, the initial attack is made by the female, usually in a crevice in the bark. The male joins the female about the time the pitch begins to flow; he then pushes the frass from the entrance hole while the female extends the gallery. After the gallery has been extended several centimeters he then packs the lower areas with frass thereby blocking the entrance hole, leaving only the area where the beetles are working free for their activities. The gallery may or may not have a nuptial chamber; ventilation tunnels may be spaced irregularly as in *brevicomis*. It has been reported (Dixon and Osgood, 1961:6) that extension of the egg gallery may occur at the rate of about 2.5 cm. per day.

Published data pertaining to the period of oviposition, egg production by individual females, and details of gallery formation are not sufficient for conclusive statements concerning them. The small amount of published information, however, permits the following comments.

Drawings, photographs (Hopkins, 1909b:58-68; Fronk, 1947:9; Dixon and Osgood, 1961:7; etc.), and limited personal observations of egg galleries indicate that egg niches are placed alternately along the sides of the gallery in contact with the cambium. They are symmetrical and about one-third as deep as the width of the gallery and slightly wider than deep. The spacing of niches appears variable, but evidently they may be as close as 6 mm., with an average of 17 mm. between niches on one side (accurate measurements should provide figures much lower than these). Eggs are deposited individually and each is packed in its niche with specially prepared frass to the original contour of the gallery.

Fronk (1947:10) found that under optimum conditions the eggs hatch in from 3 to 9 days, with an average of 5.5 days; unfavorable conditions such as occur during the winter evidently may lengthen the incubation period to several months. Each newly hatched larva mines the phloem in contact with the cambium, approximately perpendicular to the egg gallery. This mine of the first instar larva is of uniformly thin diameter for about one centimeter, or several times this length in an unfavorable environment (Hopkins, 1909: 61), it then widens abruptly into a short, irregularly oval area where the remaining larval instars are passed (Fronk, 1947:8). This enlarged area may be in contact with the cambium and visible on peeled bark, or in thick bark it may be entirely in the inner bark as in *brevicomis*. Toward the end of the fourth instar the larva bores into

the outer bark where it clears a pupal chamber and enters the quiescent prepupal stage. The larval period under optimum conditions varies from 25 to 38 days and the pupal period about 8 to 11 days (Fronk, 1947:6); either or both stages might be lengthened several months by unfavorable conditions. In Virginia the lift cycle was completed under near optimum conditions in from 40 to 54 days (Fronk, 1947:7).

The number of generations completed in one year varies from 3 to 5 in the eastern United States; in Mexico and Guatemala the number undoubtedly is greater.

Dendroctonus parallelocollis Chapuis

Figs. 7-10, 34, 48-49

Dendroctonus parallelocollis Chapuis, 1869, Synopsis des Scolytides, p. 36 (1873, Mém. Soc. Roy. Sci. Liége (2)3:244).; Blandford, 1897, Biol. Centr.-Amer., Coleopt. 4(6):147; Hopkins, 1905 (1906), Proc. Ent. Soc. Washington 7:81; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):99; Hagedorn, 1910, Coleopterorum Catalogus 4:22; Hagedorn, 1910, Genera Insectorum 111:60; Hopkins, 1915, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(2):211; Chamberlin, 1939, Bark and Timber Beetles of North America, p. 144; Schedl, 1940 (1939), An. Esc. Nac. Cienc. Biol. (Mexico) 1:339; Schedl, 1955, Zeitschr, angew. Ent. 38:11. BIOL.: Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 83(1):75; Muesebeck, 1950, Jour. Econ. Ent. 43:119, 131; Perry, 1951, Unasylva (Mexico) 5:159; Becker, 1951, Zeitschr. angew. Ent. 33:186; Becker, 1952, Trans. Ninth Internatl. Congr. Ent. 1:582; Becker, 1954. Zeitschr. angew. Ent. 36:20; Becker, 1955, Zeitschr. angew. Ent. 37:11.

Dendroctonus approximatus Dietz, 1890, Trans. American Ent. Soc. 17:28, 31; Blandford, 1897, Biol. Centr.-Amer., Coleopt. 4(6):147; Hopkins, 1905 (1906), Proc. Ent. Soc. Washington 7:81; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):101; Swaine, 1909, New York St. Mus. Bull. 134:95; Hagedorn, 1910, Coleopterorum Catalogus 4:19; Hagedorn, 1910, Genera Insectorum 111:60; Hopkins, 1915, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(2):211; Chamberlin, 1939, Bark and Timber Beetles of North America, p. 159; Schedl, 1940 (1939). An. Esc. Nac. Cienc. Biol. (Mexico) 1:322. BIOL.: Schwarz, 1902, Proc. Ent. Soc. Washington 5:32; Hopkins, 1903, U. S. Dept. Agric. Yearbook 1902:281; Hopkins, 1903, Canadian Ent. 35:61; Hopkins, 1904, U. S. Dept. Agric. Div. Ent. Bull. 48:44; Hopkins, 1904, U. S. Dept. Agric. Yearbook 1904:281; Hopkins, 1905, U. S. Dept. Agric. Bur. Ent. Bull. 56:11; Burke, 1908, Proc. Ent. Soc. Washington 9:115; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 83(1):77; Swaine, 1909, New York St. Mus. Bull. 134:95; Felt, 1924. Manual of Shade Tree and Shrub Insects, p. 251; Blackman, 1931, New York St. Coll. For., Syracuse Univ. Bull. 4(4), Tech. Pub. 36:30; Keen, 1938, U. S. Dept. Agric. Misc. Pub. 273:102; Beal, 1939, U. S. Dept. Agric. Farmers Bull. 1824:11; Muesebeck, 1950, Jour. Econ. Ent. 43:122, 131; Pearson, 1950, U. S. Dept. Agric. Monogr. 6:154; Anonymous, 1951, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv., Sup. 4:8; Anonymous, 1952. U. S. Dept. Agric. Bur. Ent. Pl. Quar. Coop. Econ. Ins. Rept. 1(4):94; Anonymous. 1954, U. S. Dept. Agric. For. Serv. For. Ins. Rept. 1954:10; Yasinski, 1956, U. S. Dept. Agric. Rocky Mtn. For. Expt. Sta. Paper 23:1.

Dendroctonus parallelocollis var. *approximatus*: BIOL.: Fall and Cockrell, 1907, Trans. American Ent. Soc. 33:145.

This species is rather closely allied to *frontalis* and *adjunctus*,

but is larger and more coarsely sculptured than either. From *frontalis* it may also be distinguished by the more nearly flattened declivital interspaces with the second weakly impressed, by the uniseriate, rounded granules on the second declivital interspace, and by the larger, more closely set crenulations of the elytral disc. From *adjunctus* it is also distinguished by the more strongly impressed declivital striae, by the interspacial granules being uniseriate only on declivital interspace two (rarely also on one) and much more closely spaced, by the much larger, more numerous crenulations of the elytral disc, and by the more prominent transverse pronotal callus of the female and large frontal, almost hornlike, tubercles of the male.

Male.—Length 4.5-7.4 mm. (average about 6.0), 2.5 times as long as wide; mature color very dark brown to black.

Frons convex, with a pair of lateral elevations on median half just below upper level of eyes separated by a deep median groove, the summit of elevations armed at their dorsomedian margins by one or two prominent, somewhat dorsomedially oriented tubercles; epistomal margin elevated, its surface smooth and shining; epistomal process slightly wider than half (0.57 times) the distance between eyes, its arms oblique (about 40° from the horizontal) and elevated, the horizontal portion about half its total width, transversely concave, ending just above epistomal margin and bearing under its distal margin a dense brush of conspicuous yellowish setae; surface punctate-rugulose above eyes, coarsely, rather deeply punctured and subgranulate below. Vestiture, in addition to epistomal brush, rather long, sparse.

Pronotum 1.4 times as wide as long, widest at base; sides feebly arcuate and converging very slightly to the almost imperceptable anterior constriction just behind the broadly, very shallowly emarginate anterior margin; surface smooth and shining, the punctures rather small, moderately deep, close (size, depth and arrangement variable in a series); a raised median line feebly indicated anteriorly. Vestiture sparse, inconspicuous; moderately long at sides.

Elytra 2.2 times as long as pronotum; sides straight and subparallel on basal two-thirds, rather broadly rounded behind; basal margins arcuate and bearing a row of about nine, moderately large, raised, overlapping crenulations, with several smaller submarginal ones particularly on interspaces two and three; striae weakly impressed, the punctures usually rather small and shallow with anterior margins raised, subcrenulate; interstriae about twice as wide as striae and armed by abundant, confused, transverse crenulations, each averaging at least half the width of an interspace, some as wide as an entire interspace on posterior half of disc. Declivity moderately steep, convex, with interspace two weakly impressed; striae narrowly, moderately impressed, the punctures smaller than on disc, distinctly impressed, one and two almost straight, three curving away from suture on upper half, toward suture on lower half; interspaces scarcely if at all convex, about equal in width (except

for expanded portion of three), each bearing a series of moderately large rounded granules, those on one and three usually confused, uniseriate on two, usually with a few to many fine punctures in addition to granules; granules on interspace two separated from one another by an average distance equal to one-half width of the interspace. Vestiture not abundant, longer on sides and declivity, the longest setae about one and one-half times as long as width of an interspace.

Female.—Similar to male except lateral elevations of frons less prominent and unarmed, with median groove consequently less conspicuous; arms of epistomal process less strongly elevated; pronotal constriction largely filled by a prominent transverse elevated callus both laterally and dorsally; punctures of pronotal disc very slightly larger and deeper; transverse crenulations of elytral disc and declivital granules somewhat larger.

Type locality.—Mexico (Colorado for *approximatus*). The type of *approximatus* was studied; *parallelocollis* was based on Hopkins' material that was compared to the type.

Hosts.—*Pinus apacheca*, *arizonica*, *ayacahuite*, *chihuahuana*, *hartwegi*, *leiophylla*, *montezumae*, *patula*, *ponderosa*, *rudis*, and *teocotl*.

Distribution.—Central Utah and Colorado south to Honduras.

Specimens from the following localities were examined (Fig. 48). ARIZONA: Black Mesa F. R., Chiricahua Mts., Flagstaff, Fort Apache, Graham Mts., Grand Canyon N. P., Kaibab N. F., Paradise, Pine, Portal, Prescott, Rincon Mts., Santa Catalina Mts., Santa Rita Mts., Show Low, Tucson, and Williams. COLORADO: Brookvale, Glen Haven, Las Animas, La Veta, Monte Vista, Palmer Lake. NEW MEXICO: Capitan Mts., Carson N. F., Cloudcroft, Lincoln N. F., Santa Fe, and Sierra Blanca. UTAH: Bryce Canyon N. P., Dixie N. F., Escalante, Kamas, Long Hollow, Panguitch, Panguitch Lake, and Pin Hollow in Fishlake N. F. CHIHUAHUA: Chuichupa, and Tres Rios. DURANGO: El Salto, and Sierra Durango. DISTRITO FEDERAL: Mexico. MEXICO: Ixtaccihuatl. MICHOACAN: Jacona. MORELOS: Jonacatepec. OAXACA: Oaxaca. Puebla: Texmelucan. TLAXACALA: Tlaxacala. VERA CRUZ: Jalapa and Vera Cruz. GUATEMALA: Quezaltenango, Santa Cruz del Quiche, and Tecpan. HONDURAS: San Pedro Sula.

Geographical variation.—Constant differences associated with geographical origin were not apparent. The features used by Hopkins (1909a:70) in establishing geographical races refer to individual differences that can be found in a long series from almost any locality throughout its range.

Biology.—This is not an aggressive species, consequently, damage caused by it is comparatively minor. It is a secondary enemy of pine, entering the host only after the tree has been overcome by the more aggressive species of *Dendroctonus* or of *Ips*.

Adults and larvae in all stages of development overwinter in their galleries at the base of the host tree, or, in the case of felled trees, on the lower side of the trunk next to the ground. They become active somewhat later than other species and usually extend their

Fig. 48. Probable geographical distribution of *Dendroctonus parallelocollis* with collection sites indicated.

old galleries for a period, with the adults resuming egg-laying activities, before emerging from the host. In the northern parts of the range the flight period begins early in June and continues until October, with the principal period of activity occurring in June and early July. In southern Mexico and Guatemala activity probably continues throughout the year without seasonal interruptions. Emergence from the host occurs gradually over a long period of time, consequently, large numbers of beetles are not in flight at the same time making a concerted attack on one tree by this species exceedingly difficult.

The trees selected for attack are those previously selected by and largely overcome by other species, or those felled more than six weeks prior to the attack. This species, usually occupies the basal portion of the bole from the ground level up to a height of six or eight feet; in the northern parts of its range, where it competes with *adjunctus* for space in the basal parts of the host, its galleries seldom extend more than two or three feet above the level of the ground. It also breeds in felled trees (Blackman 36:30), usually only on the lower side, particularly in those areas in contact with the ground. The smallest trees observed in which this species was breeding were 12 inches D.B.H., although this probably does not represent the minimum size acceptable to the species.

Ordinarily the attack is directed at the butt of the tree in areas of bark not occupied one to three weeks previously by other species. In an injured tree the attack may extend over a rather long period of time as successive generations slowly girdle it.

Basically the galleries (Fig. 49) are longitudinal and winding; they are coarser than those of associated species, particularly *adjunctus*, and present a strikingly different overall pattern. Branch galleries, many of which cross or join other galleries, are numerous, causing the entire network of galleries to form an apparently

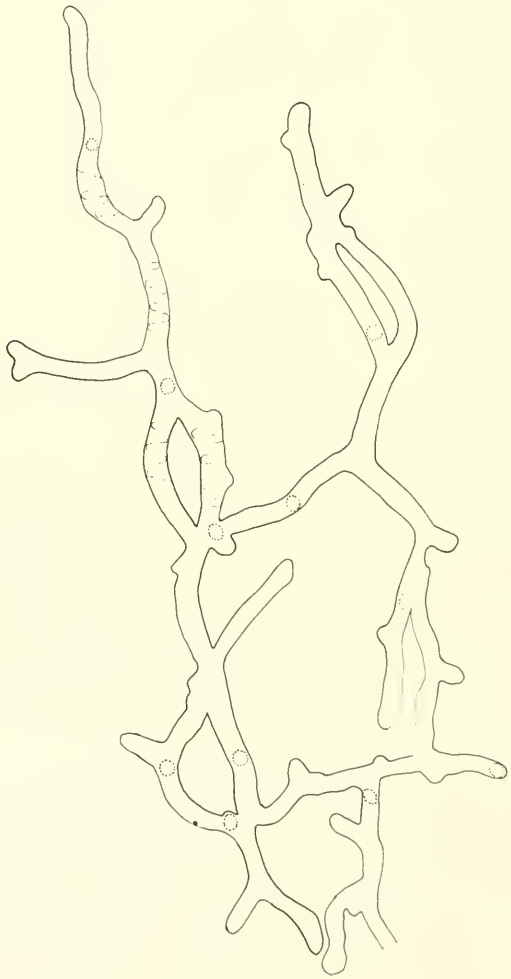

Fig. 49. *Dendroctonus parallelocollis*: Egg galleries form an apparent haphazard criss-cross pattern; egg niches large, placed alternately on gallery wall opposite cambium (upper left); larval mines entirely in outer bark, never exposed on surface of peeled bark.

aimless criss-cross pattern. As with other species the galleries are almost entirely in the inner bark, very faintly grooving or at least staining the cambium.

The egg galleries are rather coarse, averaging about 5 mm. in diameter. Gallery systems may be extensive, but because of their branching and anastomosing character it is virtually impossible to measure the work of individual beetles.

As with other species the initial attack is made by the female. Soon after she reaches the phloem tissues she is joined by the male. As with other species he then expels excess frass from the entrance hole or later packs the lower or more remote areas of the gallery with excess frass in order to keep clear the area where the female is working. Egg niches are very different from other species; they are not in contact with the cambium, but are located alternately on the sides of the wall farthest from the cambium. The niches are cup-shaped, larger than usual, and extend into the non-living portion of the bark. Each niche may contain, according to Blackman (1936:30), one to four eggs; not more than one egg per niche was found during this study. The larval mines are entirely in the bark, mostly in the outer bark, and do not contact the cambium at any time. Their length is variable and not easily measured, but evidently they are rather short. Pupal chambers are almost always in the outer bark.

Oviposition apparently begins about a week after the attack and probably continues over a substantially longer period than is the case with related species. The position of the egg niches and the possible deposition of several eggs in each makes it difficult to count with any degree of accuracy the number of eggs produced by any one female, since many of the eggs are destroyed by the observer's attempt to locate the niches. From the number of niches found, however, it is estimated that the number is not large, probably seldom exceeding 40 eggs per female. As with other species, a majority of the eggs apparently were deposited in the first third of the egg gallery. The exact spacing of egg niches, and the periods of incubation, larval and pupal development were not determined.

In the northern parts of its range one generation per year appears to be normal.

Dendroctonus adjunctus Blandford

Figs. 11-12, 35, 50-51.

Dendroctonus adjunctus Blandford, 1897, Biol. Centr.-Amer., Coleopt. 4(6):147; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):157; Hagedorn, 1910, Coleopterorum Catalogus 4:19; Hagedorn, 1910, Genera Insectorum 111:60; Chamberlin, 1939, Bark and Timber Beetles of North America, p. 144; Schedl, 1955, Zeitschr. angew. Ent. 38:8. BIOL.: Johnston, 1942, Proc. Amer. Sci. Congr. (Washington, May 10-18, 1940) 8:245; Becker, 1951, Zeitschr. angew. Ent. 33:186; Becker, 1952, Trans. Ninth Internatl. Congr. Ent. 1:582; Becker, 1954, Zeitscher. angew. Ent. 36:20-61; Becker, 1955, Zeitschr. angew. Ent. 37:1.

Dendroctonus convexifrons Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):87 (*new synonymy*); Hagedorn, 1910, Coleopterorum Catalogus 4:20; Hagedorn, 1910, Genera Insectorum 111:60; Chamberlin, 1939, Bark and Timber Beetles of North America, p. 158; Schedl, 1940 (1939), An. Esc. Nac. Cienc. Biol. (Mexico) 1:339. BIOL.: Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 83(1):53; Felt, 1924, Manual of Shade Tree and Shrub Insects, p. 252; Blackman, 1931, New York St. Coll. For., Syracuse Univ. Bull. 4(4), Tech. Pub. 36:29; Keen, 1938, U. S. Dept. Agric. Misc. Pub. 273:102; Beal, 1939, U. S. Dept. Agric. Farmers Bull. 1824:11; Pearson, 1950, U. S. Dept. Agric. Monogr. 6:154; Anonymous, 1951, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest. Surv., Sup. 4:8; Anonymous, 1952, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Coop. Econ. Ins. Rept. 1(4):94; Anonymous, 1955, U. S. Dept. Agric. For. Serv. For. Ins. 1954:10; Yasinski, 1956, U. S. Dept. Agric. Rocky Mtn. For. Expt. Sta. Paper 23:1.

Dendroctonus approximatus: Dietz, 1890, Trans. American Ent. Soc. 17:31 (part); Schwarz, 1902, Proc. Ent. Soc. Washington 5:32 (part).

This species occupies a position between the two major groups within the genus, more or less compromising the characters of *parallelocollis* and *ponderosae*. Although the relationship is not close, it is allied to *parallelocollis*, but is readily distinguished by the more slender body form, by the more widely spaced, uniseriate granules on the first three declivital interspaces, by the more finely sculptured elytral disc, and by the absence of frontal tubercles in the male and more poorly developed transverse pronotal callus in the female. In many respects it is similar to *ponderosae* but may be distinguished by the more slender form, by the smooth, shining declivital interspaces, by the stronger median frontal groove, and, in the female, by the transverse pronotal callus.

Male.—Length 3.8-6.0 mm. (average about 5.2), 2.65 times as long as wide; mature body color rather dark brown.

Frons convex, with a pair of unarmed lateral elevations on median half just below upper level of eyes separated by a rather inconspicuous median groove; epistomal margin elevated, its surface smooth and shining; epistomal process half (0.50 times) as wide as distance between eyes, its arms oblique (about 40° from the horizontal) and elevated, the horizontal portion about half its total width, transversely concave, ending just above epistomal margin and bearing under its distal margin a dense brush of conspicuous yellowish setae; surface punctate-rugulose above eyes, more deeply punctured and subgranulate below. Vestiture, except epistomal brush, sparse, inconspicuous, rather long.

Pronotum 1.4 times as wide as long, widest on basal third; sides rather strongly arcuate on basal three-fourth, rather strongly constricted behind the broadly, shallowly emarginate anterior margin; surface smooth with rather fine, shallow, close punctures on median third, becoming more finely punctured laterally; an indistinct median line apparent. Vestiture rather sparse, long, becoming coarse laterally.

Elytra 2.5 times as long as pronotum; sides straight and subparallel on basal two-thirds, rather narrowly rounded behind; basal margins arcuate and bearing a row of about nine, moderately

large, raised, overlapping crenulations, with several smaller submarginal ones particularly on interspaces two and three; striae weakly impressed, the punctures rather small and shallow; interstriae about twice as wide as striae and armed by rather abundant confused, transverse crenulations, each averaging about one-half the width of an interspace, a few almost as wide as the interspace on posterior half of disc. Declivity moderately steep, convex, with interspace two weakly impressed; striae weakly impressed, the punctures greatly reduced, one straight, two curving slightly toward suture on lower third, three diverging from suture on upper half, curving toward suture on lower third; interspace one slightly raised, two impressed and flat, three feebly convex, each bearing a uniseriate row of sparse, rounded or pointed granules and in addition several confused, minute punctures; granules on two separated from one another by an average distance equal to width of the interspace. Vestiture rather sparse, longer on sides and declivity, the longest setae about one and one-half or two times as long as width of an interspace.

Female.—Similar to male except lateral elevations and median frontal groove poorly developed; arms of epistomal process less strongly elevated; pronotal constriction with a feebly developed transverse elevated callus; punctures of pronotal disc very slightly larger and deeper; and transverse crenulations of elytral disc and granules of declivity very slightly larger.

Type locality.—Totonicapam, Guatemala (Williams, Arizona, for *convexifrons*). The type of *convexifrons* was studied; the type of *adjunctus* was compared to my material by R. T. Thompson.

Hosts.—*Pinus ayacahuite*, *chihuahuana*,, *montęzumae*, *ponderosae*, *pseudostrobus*, *rudis*, and *tenuifolia*.

Distribution.—Southern Utah and Colorado south to Guatemala.

Specimens from the following localities were examined (Fig. 50). ARIZONA: Flagstaff, Fort Apache, Graham Mts., Grand Canyon N. P., Jacobs Lake, Kaibab N. F., Paradise, Rustler Park, Santa Catalina Mts., Show Low, and Williams. COLORADO: Durango, Ft. Garland, Las Animas Co., La Veta, Monte Vista, Rye, San Isabel N. F., and "Vallecito R. S." NEW MEXICO: Capitan, Carson N. F. Cloudcroft, Ft. Wingate, "Hermit Peak," Las Vegas, Lincoln N. F., Sierra Blanca Mts., and Vermejo. UTAH: Escalante, Long Hollow in Dixie N. F., Manti-LaSal N. F., Panguitch Lake, and Sanford Canyon. MEXICO: Nevado de Toluca, and Penuela La Gavia. GUATEMALA: Cerro Quemado, Chuchumatanes, Guatemala, La Esperanza, Las Trojadas, Montana de las Nubes, Poptum, Quetzaltenango, Sierra Maria Tecum, Tecpn, and Totonicapan.

Geographical variation.—Not observable in the limited material at hand.

Biology.—This species generally works in concert with other species of *Dendroctonus* to overcome a tree. Its galleries resemble, superficially at least, those of other species and, consequently, the resulting misidentifications have attributed much of the damage actually done by this species to others having more formidable repu-

Fig. 50. Probable geographical distribution of *Dendroctonus adjunctus* with collection sites indicated.

tations as tree killers. In the absence of an epidemic of other species it appears much more aggressive than the available literature would indicate, frequently initiating the primary attack on a tree.

Although any stage of development may be represented, the winter usually is passed as half grown larvae or as adults starting a new attack in the fall but without commencing oviposition. Larval development is resumed and egg deposition is started or resumed as soon as spring temperatures become sufficiently high. The brood, both young adults and larvae, completes its development and begins to emerge to seek new hosts in May or early June, usually several weeks after the emergence of *brevicomis* and *ponderosae*. Its habits of commencing attacks in the fall and the late emergence in the spring are important factors in the apparent lack of aggressiveness of this species, since the timing of its flight activity coincides with the period when other species have overcome host trees but have not yet occupied the lower portions of the bole. Although some flight activity occurs throughout the summer months, two periods of increased activity occur. The first is in May and early June, the second and greatest occurs between the latter part of August and the middle of October. The attack on a particular tree is spread over a considerable period of time and usually involves a relatively small population of this species.

Trees selected for attack are weakened standing trees larger than about ten inches D. B. H. Galleries have been observed in stumps, but not in prostrate trees or logs. In the absence of competing species the area of attack may extend from ground level to a height of about 10 or 12 feet. When competing species, particularly *pondero-*

sae, are present in large numbers this species may be restricted to less than the lower three feet of the bole.

The attack appears to begin in the upper parts of the area occupied by this species; that is, the bole about 4 to 12 feet above the ground level, with successively newer attacks occurring below this area until the level of the ground is reached. The attack may be completed in a few days when populations are high, or it may ex-

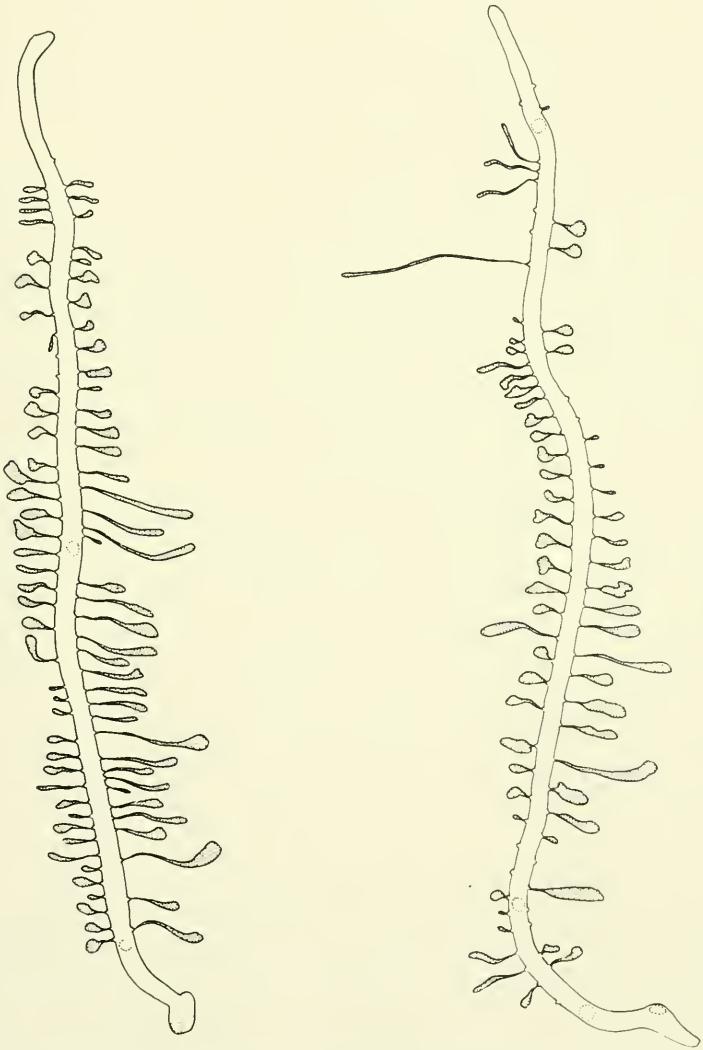

Fig. 51. *Dendroctonus adjunctus*: Egg galleries slightly to rather strongly sinuate (example at right about average); individual egg niches placed alternately on sides of gallery; larval mines transverse, usually in cambium but may extend into outer bark, seldom cross one another.

tend over the greater part of a year, particularly when the first attacks are made in the fall.

Egg galleries (Fig. 51) are sinuous and almost always extend upward from the entrance hole. As with other species of this genus they are almost entirely in the phloem, very lightly scoring or at least staining the wood. The total longitudinal displacement of an egg gallery usually is about three to four times as great as the total lateral displacement. Ordinarily the gallery extends horizontally either right or left from the entrance hole about four to seven centimeters then curves upward; about two to four broad sinuous curves are included in its vertical ascent. From the principal longitudinal axis of the gallery the first of these curves diverges about four to six centimeters, the remaining curves diverge about one-half to two centimeters from this axis. Of 36 egg galleries studied in the Panguitch, Utah, area during the last week of June, 1960, the average gallery length was 31 cm., the maximum was 89 cm.; the average width was about 4 mm. Although it appeared that an effort was made by the beetles to avoid doing so, galleries did cross or anastomose occasionally. Approximately one gallery in 25 descended vertically, evidently to avoid crowding or crossing neighboring galleries; more rarely one was primarily transverse. Branching or side galleries extending from the main egg tunnel were uncommon. When such branches did occur they usually did not exceed three centimeters in length and did not contain egg niches.

The initial attack is made by the female. As with other species this usually occurs in a crevis of the bark; ordinarily she is joined by the male about the time the entrance tunnel reaches the cambium. The male, as with other species, ejects frass from the entrance hole while the female extends the gallery. When sufficient working space is available he then packs the lower portions of the gallery with the excess frass.

Ventilation tunnels occur at irregular intervals; the minimum observed distance between two of them was 1.7 cm.; in trees having relatively thin bark they may be entirely absent. The average distance between ventilation tunnels in the 36 galleries measured for this study, was 5.2 cm. The first most commonly is placed within one centimeter, either above or below, the first egg niche; the average distance from the entrance hole to the first egg niche was 3.5 cm.

Egg niches are arranged alternately in the phloem on the sides of the gallery in contact with the cambium. Each is symmetrical, slightly deeper than wide and, compared to the foregoing species, is rather small. Each niche is very slightly larger than the egg it contains. The number and spacing of egg niches is variable; the minimum observed distance between two niches located on the same side of a gallery was 1.5 mm., the average distance was about 3.5 mm. The average number of egg niches in the 36 galleries mentioned above was 44.1; the maximum was 119. About one-tenth of the niches were located exactly opposite one another on the different

sides of the gallery; this was a notable departure from the consistently alternate placement of niches in the preceding species where such an occurrence was exceedingly uncommon. Eggs are deposited individually in the niches; each niche is then filled by specially prepared frass to the original level of the gallery.

The period of incubation has not been determined precisely, but evidently it requires about a week under optimum conditions. The newly hatched larvae construct narrow tunnels in the cambium region perpendicular to the egg gallery. The larval mine extends about one to four centimeters along a straight to winding route, without increasing in diameter. It then expands abruptly into an oval to irregular feeding chamber approximately one-half to one centimeter wide and about one or two centimeters long. The entire larval mine usually is in contact with the cambium and is visible on the inner bark. Some of the larvae pupate in this chamber, however, most of them mine into the outer bark for pupation.

The number of generations may vary from one complete and a partial second generation per year to one generation in two full years (Hopkins 1909b:55). Although not reported, it appears possible that two generations might be completed in favorable years and localities in the southern parts of its range.

Dendroctonus ponderosae Hopkins

Figs. 13, 36, 52-53.

Dendroctonus ponderosae Hopkins, 1902, U. S. Dept. Agric. Div. Ent. Bull. 32:10; Hopkins, 1902, Proc. Ent. Soc. Washington 5:3; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):109; Swaine, 1909, New York St. Mus. Bull. 134:98; Hagedorn, 1910, Coleopterorum Catalogus 4:22; Hagedorn, 1910, Genera Insectorum 111:60; Hopkins, 1915, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(2):211; Swaine, 1918, Dom. Canada Dept. Agric. Ent. Br. Bull. 14(2):65; Chamberlin, 1939, Bark and Timber Beetles of North America, p. 156. Biol.: Hopkins, 1902, U. S. Dept. Agric. Div. Ent. Bull. 37:21; Hopkins, 1903, U. S. Dept. Agric. Yearbook 1902:275, 282; Hopkins, 1903, Canadian Ent. 35:59; Gillette, 1903, Colorado Agric. Rept. 24:118; Hopkins, 1904, U. S. Dept. Agric. Div. Ent. Bull. 48:41, 43, 44; Hopkins, 1905, U. S. Dept. Agric. Yearbook 1904:275, 281; Hopkins, 1905, Proc. Ent. Soc. Washington 7:147; Hopkins, 1905, U. S. Dept. Agric. Div. Ent. Bull. 56:10; Currie, 1905, U. S. Dept. Agric. Div. Ent. Bull. 53:100; Burke, 1906, Proc. Ent. Soc. Washington 7:4; Hopkins, 1906, Proc. Ent. Soc. Washington 7:147; Hopkins, 1906, Proc. Ent. Soc. Washington 8:4; Webb, 1906, U. S. Dept. Agric. Yearbook 1905:631; Webb, 1907, U. S. Dept. Agric. Yearbook 1906:515; Howard, 1907, U. S. Dept. Agric. Div. Ent. Rept. 1906:13; Hopkins, 1908, U. S. Dept. Agric. Yearbook 1907:162, 548; Hopkins, 1908, West Virginia Lumberm., Jan. 10:11; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 58:59, 76; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 83(1):90; Hopkins, 1909, U. S. Dept. Agric. Yearbook 1908:574; Hopkins, 1910, U. S. Dept. Agric. Bur. Ent. Circ. 125:2; Howard, 1910, U. S. Dept. Agric. Bur. Ent. Rept. 1909:21; Hopkins, 1912, U. S. Dept. Agric. Bur. Ent. Circ. 142:7; Butterick, 1912, Jour. Econ. Ent. 5:456; Swaine, 1913, Ontario Ent. Soc. Rept. 43:90; Brues, 1920, Insects and Human Welfare, p. 70; Miller, 1923, Timberman 26(2):50; Felt, 1924, Manual of Tree and Shrub Insects, p. 256; Craighead, 1925, Jour. Forestry 23:347; Craighead, 1927, U. S. Dept. Agric. Circ. 411:7; Nelson and Beal, 1929, Phytopathology 19:1101; Craighead,

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This distinctive species appears to be more closely allied to *adjunctus* than to others in the genus, but is readily distinguished by the absence of lateral frontal elevations and a median groove, by the opaque surface of the elytral declivity, by the impressed declivital striae, by the stout body, and, in part, by the distribution (Fig. 52).

Male.—Length 3.7-7.5 mm. (average about 5.5; size evidently dependent on moisture conditions regulated by thickness of bark of host tree), 2.3 times as long as wide; mature body color black.

Frons convex from eye to eye, from vertex to epistoma, median line narrowly impressed above upper level of eyes, rather broadly protrubrant over an indefinite median area below upper level of eyes, often with remnants of a narrowly impressed median line; epistomal margin elevated, its surface smooth and shining; epistomal process half as wide (0.50 times) as the distance between eyes, its arms oblique (about 30° from the horizontal) and elevated along their median halves, the horizontal portion about half its total width, transversely concave, overlapping and ending just above epistomal margin and bearing under its distal margin a dense brush of conspicuous yellowish setae; surface punctate-rugulose above eyes,

coarsely, rather deeply punctured and subgranulate below. Vestiture, in addition to epistomal brush, rather long, sparse, inconspicuous.

Pronotum 1.4 times as wide as long, widest at base; sides feebly arcuate, almost straight on basal two-thirds, converging slightly toward the well developed constriction just behind the broadly, shallowly emarginate anterior margin; surface smooth, shining, with very close, rather small, moderately deep punctures (variable), becoming granulose laterally; a median line feebly indicated, more prominent anteriorly. Vestiture scanty, usually evident only at sides.

Elytra 2.1 times as long as pronotum; sides straight and subparallel on basal two-thirds, rather broadly rounded behind; basal margins arcuate and bearing a row of about nine, moderately large, raised, overlapping crenulations, with several smaller submarginal ones particularly on interspaces two and three; striae weakly impressed. the punctures rather small, rather deep; interstriae about twice as wide as striae and armed by rather coarse, confused, transverse crenulations, each averaging about half the width of an interspace. Declivity rather steep, convex, with interspace two rather strongly impressed; striae rather narrowly impressed, the punctures smaller than on disc; striae one slightly, two rather strongly, three very strongly curved toward suture; interstriae usually at least slightly convex, minutely rugulose, dull, the punctures fine, confused, distinct to obscure or subgranulate; each interspace with a sparse, more or less definite median row of rather large granules. Vestiture scanty, longer and more conspicuous on declivity, longest setae slightly longer than a distance equal to width of an interspace.

Female.—Very similar to male, but evidently epistomal process less well developed, and elytral crenulations and declivital granules a little larger.

Type locality.—Spearfish, South Dakota (Kootenai, Idaho, for *monticolae;* and Little Yosemite, California, for *jeffreyi*). The types of all three descriptions were studied.

Hosts.—Pinus albicaulis, balfouriana, contorta, coulteri, edulis, flexilis, jeffreyi, lambertiana, monophylla, monticola, murrayana, ponderosa, and strobiformis. During an epidemic it was recorded from *Picea engelmanni.*

Distribution.—Southern British Columbia to the Black Hills of South Dakota, and south to northern Mexico.

Specimens from the following localities were examined (Fig. 52). ARIZONA: Chiricahua Mts., "Crook N. F.," Flagstaff, Fredonia, Kaibab N. F., and San Francisco Mts. CALIFORNIA: "Alder Ck.," Anthony Ck., Bass Lake, Bear Ck. R. S., Ben Lomond, Big Bear Lake, Big Bend, Big Meadows, Blacks Mt., Blue Canyon, Bray, Bunnel, Burnt Corral Meadows, Butte Lake, Carrville, "Cassidy Ridge," Cecilville, Chester, "Chiquito Basin," Clover Valley, Coulterville, Cow Ck., Crestline, Crocker R. S., Deep Ck., Dorrington, Duck Lake, Eagleville, Echo Lake, Eiler Lake, Facht, Fallen Leaf Lake, Favingers Camp, Fawn Ck., Floriston, Ft. Jones, Fulda, "Gasquet R. S.," General Grant N. P.,

Fig. 52. Probable geographical distribution of *Dendroctonus ponderosae* with collection sites indicated.

Gordon Meadow, "Grant Pk.," Grassy Lake, "Gray Meadows," "Gray Mesa," Hackamore, Haeckle's, Hat Ck., Hoffman, Hope Valley, "Huckleberry Meadow," Hume, Huntington Lake, Inyo Co., Idyllwild, "Kangaroo R. S.," Kern Co., King's Ck. Rd., Kyburz, Laguna Mt., Lake Almanor, Lake Arrowhead, Lake Ostrander, Lake Tahoe, Lake Valley R. S., Lamoine, "Leland Meadow," Lemon Canyon, Lion Meadow, "Little Kern," Little Shasta, Little Yosemite, Lloyd Meadows, Lookout, Lush Meadows, Mammoth, Mariposa Grove, Massack Mill, Mather, McCloud, "McCreary," Medicine Lake, Miami R. S., Middle Fk. Eel River, "Millwood," Mineral, Moffit Ck., Mohawk, Moraine, Mt. Brewer, Myers, Nevada City, North Fork, Norval Flats, Ockenden, Onion Valley, "Painted George," Pinecrest, Placerville, Plantation, Pollock Pines, Pyramid R. S., Robbers Ck., "Round Meadow," "Samson Flat," San Bernardino Mts., San Gabriel Canyon, "Saples Flat," "Scoffold," "Self R. S.," Sequoia N. P., Shaver, Sisson, "Snowline Camp," Soda Springs, "Soquel Basin," "Squaw Dome," Stirling City, "Summerdale," Summit Lake, "Swaines," Tallac, Tenaya Lake, Three Rivers, Timber Mt., Tioga Rd., Trinity N. F., Wawona, "Willow Meadows," Willow Ranch, "Woodward Ck.," "Wright's Lake," Yreka, and Yuba Gap. COLORADO: Bailey, Brookvale, Cascade, "Cat Mt.," Cuchetopa, Durango, Eagle, Elictra Lake, Estes P., Florissant, Ft. Garland, Glenwood Springs, Gunnison N. F., Gould, Green Mt. Falls, Hahns Pk., Husted, Idaho Springs, "Indian Ck.," Jones Ranch, "Kennedy Sta.," Larkspur, Las Animas, La Veta, Longs Pk., Manitou, Medicine N. F., Meeker, Monte Vista, Montrose, Montezuma N. F., "Ouray N. F.," Pogosa Springs, Palmer Lake, Pikes Pk., Pine, Pingre Pk., Poncho Springs, Porter, Saguache, San Isabel, San Juan Co., San Juan N. F., Uncompahgre N. F., "Ute Pass," Westcliffe, and White River N. F. IDAHO: Cedar Mt., Centerville, Coeur d'Alene, Coeur d'Alene N. F., Collins,

Kootenai, "Moscow Mts.," Sandpoint, Smith's Ferry, and Weiser. MONTANA: Apgar, Bigfork, Blackfeet Indian Res., Columbia Falls, Helena, "Iron Mt.," Lame Deer, Lewis and Clark N. F., Logan Pass, Lolo, Madison N. F., Missoula, Saltese, and Sula. NEVADA: Baker, Crystal Bay, Glenbrook and Las Vegas. NEW MEXICO: Gila N. F., Tres Ritos, and Vermejo P. OREGON: Ashland, "Auburn," Austin, Baker, Bly, Buck Lake, Cold Springs, Crater Lake N. P., Diamond Lake, Elk Ck., "Ferris Ranch," Grants Pass, Haines, "Highland Mine," Joseph, Keno, Klamath Falls, Klamath Indian Res., "Loves Sta.," Meryl Ck., North Powder, Ochoco N. F., Pinehurst, "Pokegama," Round Lake, Sparta, Sumpter, and Wallowa. SOUTH DAKOTA: Black Hills, Custer, Deadwood, Elmore, Hill City, Lead, Nemo, Piedmont, and Sylvan Lake. UTAH: Ashley N. F., Bryce Canyon N. P., Duck Lake, Escalante, Kamas, Logan Canyon, Manti-LaSal N. F., Panguitch Lake, Uintah and Ouray Indian Res., Wasatch Mts., and Wasatch N. F. WASHINGTON: Crescent Lake, Dayton, Fairfax, "Kamiak Butte," Longmire Spring, Metaline Falls, Moran, Mt. Rainier, Mt. Rainier N. F., Northport, "Pialschie," Pullman, Randle, Seattle, Spokane, Washington N .F., and White River. WYOMING: Bear Lodge in Black Hills N. F., "Downington," Elk Mt., Encampment, Fremont Lake, "Keystone," North Fork, and Wapiti. ALBERTA: Edmonton. BRITISH COLUMBIA: Adams Lake, Alleyne Lake, Arrowhead, Aspen Grove, Babine Lake, Blue River P. O., Big Loon Lake, Cowichan Lake, Downie Ck., Forester Ck., Frances Ck., Grand Forks, "Hope Mts.," Kamloops, Kootenay N. P., Little Fish Ck., Little Shuswap Lake, Midday Valley, Morrison Lake, Mud Lake, Na Kusp, "Nehalliston For.," Peachland, Princeton, Puntchesakut Lake, Revelstoke, Seymour Narrows, Shuswap Lake, Steamboat Mt., Sugar Lake, Sugarloaf Mt., Takla Lake, Tarnezell Lake, "Trepan Ck.," Trout Lake, Upper Arrow Lake, Whitetail Lake, Windermere, and Yoho N. P. BAJA CALIFORNIA: Sierra San Pedro Martir.

Geographical variation.—Specimens from the southeastern parts of the range tend to average considerably larger than specimens from the northwestern areas. The explanation for this, however, appears to be at least partly environmental rather than genetic, since most of the specimens from southeastern areas are from *Pinus ponderosa*, a host in which greater size is normally attained from all areas, while those from the northwestern areas are mostly from other host species. It was apparent after examining numerous series from the various host species that a particular average size was more or less characteristic of a host species. The average size in a particular tree appeared to be correlated with the average thickness of the bark of the host.

There are conspicuous differences in the size and depth of pronotal punctures in almost any series. In specimens from California they tend to average much smaller and shallower than from other areas. This variation in California appears to be associated with geographical origin, intensifying gradually from north to south (Lassen N. F. to the Yosemite area), rather than with host as reported by Hopkins (1909a:71), since large specimens with very small shallow punctures, the distinguishing features of Hopkins' *jeffreyi*, can be found in series from any host of this species in California.

BIOLOGY.—This has been referred to (Craighead et al., 1931: 1009) as the most destructive species of *Dendroctonus*. Estimates of losses in our timber resources due to this insect are scattered, conflicting and confused by the fact that this species has been known concurrently by three separate scientific names. Considering all

factors, the average annual loss attributed to it since 1895 possibly may approach two billion board feet.

For the most part the winter is passed as second and third instar larvae, although a few parent adults may survive hibernation and a few larvae may reach the prepupal stage. Activity is resumed in the spring whenever temperatures become sufficiently high, probably about 50°F. A small fraction of the overwintered parent adults may resume egg laying activity in the spring, but usually most of them extend their galleries without ovipositing; very few of them re-emerge. Ordinarily by mid-June half of the immature stages have pupated (Blackman, 1931:14) and by mid-July most have matured. The young adult beetles do not emerge immediately from the brood tree, but enlarge the pupal chamber, often removing sufficient of the inner bark that their excavations join one another. One of these enlarged chambers may contain as many as 50 beetles. The period of flight is concentrated, seldom beginning before July 15 and rarely continuing later than August 25. In those areas of California where more than one generation occurs each year there may be notable departures from the usual activity cycle. Whether these deviations are the result of genetic or ecological factors is uncertain.

Trees selected for attack by endemic populations of this insect usually are overmature or weakened standing trees larger than six inches D. B. H. Windfalls or cull logs occasionally may provide favorable breeding places (Evenden, 1943:7), particularly when the bole is inclined. During epidemics the more vigorous, rapidly growing trees may be preferred (Beal, 1939:2), and coniferous host species not belonging to the genus *Pinus* may be attacked. Under endemic conditions the area of a particular tree attacked by this species may be restricted or forced upward from the base of the bole by such competing species as *adjunctus*, or downward from upper parts of the bole by *brevicomis*. Under endemic conditions in a given area the local population may exhibit a strong preference for one host species even though other acceptable host species may be intermixed. The preferred host in a given area may be Ponderosa, Lodgepole, Limber, Western white, Jeffrey or other pine species. In a given area during an epidemic any acceptable host, or sometimes any conifer, may be attacked, but following the epidemic the attacks may or may not be confined to the same host species originally favored. Climatic factors or competition usually re-establish the original conditions, however. These local races perhaps may indicate the existence of genetic factors that could lead to the formation of distinct species of beetles, but all available data suggests that the present stage of their evolution has not reached the point where geographical races (subspecies) can be recognized.

The attack evidently may follow either of two patterns depending on the age and vigor of the host tree and on the presence or absence of certain competing species of bark beetles. In mature sugar pine where aggressive competing species are virtually absent, the attack usually begins in the upper crown; the lower sections of

the tree may then be attacked by one or more successive generations over a period of two or more years (Evenden, 1943:9). In younger trees of this and other species the attack usually begins at or near the base and extends upward. Compared to other species the attack is concentrated into a relatively short period of time. It coincides with the period of emergence from about July 15 to August 25, seldom requiring more than five weeks and possibly requiring as little as three or four days during an epidemic. The beetles strike the tree individually, not in dense swarms as some popular accounts of the attack might suggest. According to Blackman (1931:21) the number of entrance tunnels per square foot of bark surface of a successful attack on an average tree ranges from about four to nine. He also observed that the number of attacks was higher in trees where four to nine trees were killed in a group (5.90 per sq. ft.) than where only one to four trees were killed in a group (5.23 per sq. ft.

The vertical linear egg galleries (Fig. 53) usually are almost straight, although occasionally an environmental peculiarity may cause some to wind slightly. They are constructed primarily in the soft inner bark or phloem, continually in contact with the cambium and very lightly scoring the wood.

The diameter of an individual egg gallery is slightly greater than the width of the beetle which constructed it. Its length varies considerably, but evidently it depends more on enivronmental than on hereditary factors. In Lodgepole pine on the Wasatch National Forest in Utah, 35 egg galleries selected at random averaged 32.6 cm., the maximum length was 67.5 cm.; in Ponderosa pine on the Dixie National Forest in Utah, 35 egg galleries averaged 47.5 cm., the maximum length was 79.0 cm. Both series of measurements were made in drought areas in July 1960. In June of 1961 similar measurements made in Jeffrey pine on the Tahoe National Forest in California, averaged 41.7 cm. for 35 galleries, with the maximum length 66.0 cm. Measurable galleries in Ponderosa pine in California and Oregon and in Western white pine in Oregon gave comparable results, but were too few in number to provide reliable data. Presumably the character of galleries observed during a severe epidemic of this species in the Black Hills area led Hopkins (1909a: 112) to assume that a completely different species existed in that area as compared to an endemic Pacific Coast form which apparently constructed much longer galleries. Actually, under endemic conditions in comparable environments, the eastern, western, northern and southern populations appear indistinguishable when measurements, bark samples or photographs of gallery systems are compared.

The initial attack is made by the female, usually in a crevice of the bark. About the time she reaches the cambium tissues where the pitch begins to flow she is joined by the male who then assists her by pushing the excavated frass out of the entrance hole. Continuation of the egg gallery is performed entirely by the female

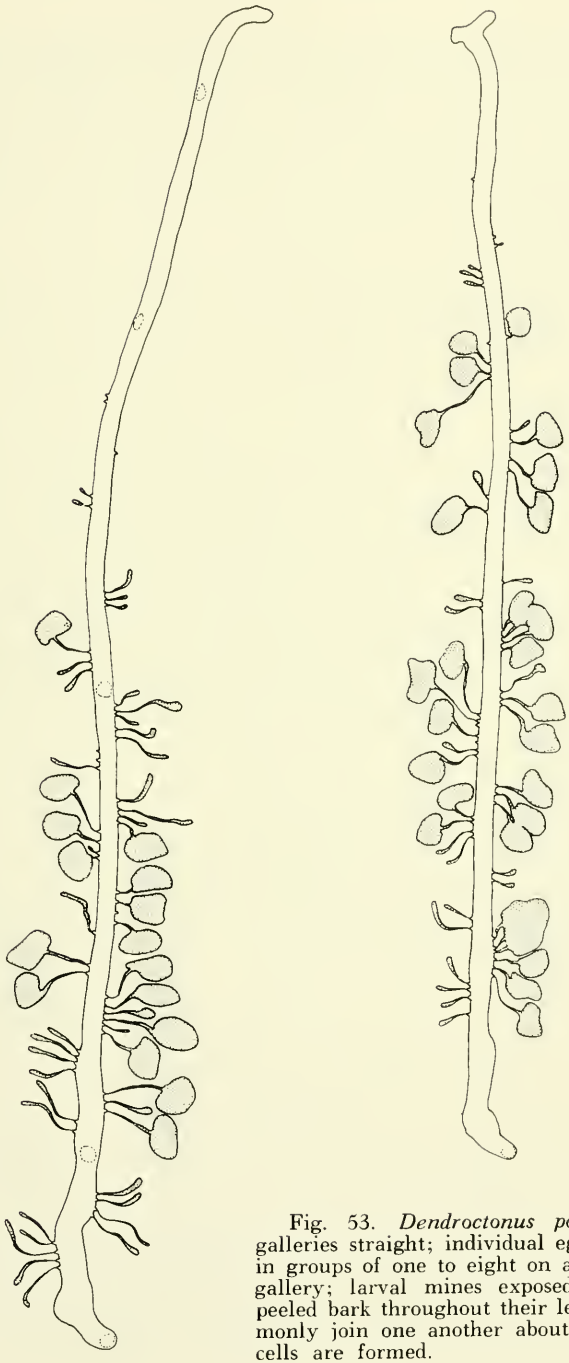

Fig. 53. *Dendroctonus ponderosae*: Egg galleries straight; individual egg niches placed in groups of one to eight on alternate sides of gallery; larval mines exposed on surface of peeled bark throughout their length, they commonly join one another about the time pupal cells are formed.

beetle. After several centimeters of gallery have been cleared and the frass ejected from the entrance hole, the male then packs the frass in the lower regions of the gallery thereby closing the entrance hole and tightly filling the gallery except for a few centimeters in the area where the beetles are working. It is not uncommon, following mating, for the male to leave the gallery, either before the entrance is blocked or through a ventilation tunnel, in order to join a second female.

From the entrance hole the gallery usually ascends diagonally about three to five centimeters before turning directly upward. In about half of the gallery systems studied this diagonal portion extended to the right of the entrance hole, about a third went to the left, and in the remainder the diagonal portion was absent. This oblique part of the tunnel ordinarily is more irregular in width than the remainder of the egg tunnel and ordinarily is sufficiently wide to permit turning or to act as a nuptial chamber. Ventilation tunnels usually are placed at irregular intervals along the egg gallery, but are not always present. Their presence appears to be related to the stage of gallery construction, to the thickness of the bark, and to the activity of the beetles. Evidently they are not constructed until after the entrance has been plugged. In thin barked Lodgepole pine 18 of the 35 galleries measured (see above) included ventilation chambers, of these 18 only three contained more than two ventilation tunnels, the maximum number was four in one gallery. In the relatively thick-barked Ponderosa pine 33 of the 35 galleries measured (see above) included ventilation tunnels and only three of the 33 included fewer than five; the maximum number in one gallery was 13.

The initial part of gallery construction progresses rapidly. Oviposition usually begins when the gallery is about one or two centimeters above the oblique portion, probably about four to five days after the attack. Egg-laying evidently continues until interrupted by cold weather. The eggs are deposited individually in comparatively small niches, although it is not uncommon for two eggs to be in one niche.

Egg niches are comparatively small, each is just large enough to accommodate an egg and a very small amount of specially prepared frass. The niches are both narrower and more shallow than those of the foregoing species. They are distributed in a pattern peculiar to this species, with alternating groups of one to eight niches placed along the sides next to the cambium. The size and spacing of these groups varies tremendously from gallery to gallery and even within the same gallery, depending upon the prevailing environmental conditions. Ordinarily about half of these "groups" consist of one niche each, seldom do they exceed five in number. It is not uncommon for one or two niches to occur opposite one of these groups, a departure from their strictly alternate arrangement. In a third of the galleries studied there were no niches in the upper or last half of the gallery; in an additional one-tenth there were

none in the last third. When niches occurred in the terminal regions of the gallery it appeared, in many cases, that the adult female either abandoned the gallery prior to the onset of cold weather or died before or during the winter months.

Following oviposition the parent beetles may continue the gallery, often ending it in a somewhat irregular feeding tunnel, or they may abandon the gallery in order to commence a new attack. Evenden (1943:12) estimated that 10 to 30 percent of the parent adults from sugar pine and almost 100 percent of those from western white pine re-emerged in order to begin a second attack. These values appear to be higher than the estimated re-emergence rate observed during this study, but support the observation that there is a greater tendency for re-emergence to occur when the bark of the host tree is either comparatively thin or subject to rapid drying for various other reasons.

The length of the incubation period has not been determined precisely, but has been estimated by various workers to require about seven to ten days. The larval mines are continuously in contact with the cambium and are somewhat irregular, but usually their main axis tends to be perpendicular to the egg gallery. Their length varies considerably with the amount of moisture or crowding present. They may be only one or two centimeters in length, increasing very slightly in width before reaching the suddenly expanded irregular feeding area where the last two or three instars and pupation are passed, or they may extend 10 or 20 centimeters and increase substantially in width before the pupal cell is encountered. It is not uncommon to find both extremes in the same system of galleries. The larvae may pass the winter in any instar, but apparently second and third instar larvae predominate. Because of overwintering in this stage and, since only one generation occurs each year, the average length of the larval period is near 300 days. During the latter part of the larval period a pupal cell is cleared of the frass in the enlarged feeding area, still in contact with the cambium. Here the prepupal and pupal stages are passed, the latter evidently requiring about two to four weeks for completion. A maturation period of about one month usually follows the pupal stage before emergence occurs.

Dendroctonus aztecus, new species

Figs. 24-26, 54.

Dendroctonus adjunctus: Gibbson and Carrillo, 1959, Sec. Agric. Ganderia Foll. Misc. 9:141.

It is presumed that many of the records published as *adjunctus* since Blandford's description refer, at least in part, to this species.

Superficially this species appears to be more closely allied to certain species of *Blastophagus*, *Pachycotes*, *Hylurgus* and *Hylurgonotus* than to other species of *Dentroctonus* and, in many respects,

appears to resemble the hypothetical ancestor of this genus. Although definitely more primitive, it is, however, rather closely allied to *terebrans* from which it differs by the flat epistomal process, by the more broadly, evenly convex frons, by the subcylindrical pronotum without a conspicuous anterior constriction, by the more coarsely sculptured elytral disc, and by the distribution (Fig. 54).

Male.—Length 5.5 mm. (paratypes 5.2-6.9), 2.65 times as long as wide; mature body color black.

Frons almost uniformly convex between eyes from vertex to epistomal process, with a small, rather indefinite median impression on lower third well above base of epistomal process; epistomal margin elevated, its surface smooth and shining; epistomal process slightly narrower than half (0.44 times) the distance between eyes, its lateral margins oblique (about 45° from the horizontal) and not at all elevated, the horizontal portion slightly more than half its total width, flat, overlapping and very slightly exceeding epistomal margin and bearing under its distal margin a dense brush of conspicuous yellowish setae; surface rather coarsely, closely, deeply punctured with rather abundant, isolated granules interspersed. Vestiture, in addition to epistomal brush, moderately long, sparse, inconspicuous.

Pronotum 1.2 times as wide as long, widest on basal half; sides weakly arcuate, almost subparallel on basal half, then converging gradually to the rather poorly developed transverse constriction just behind the broadly, shallowly emarginate anterior margin; surface smooth and shining with moderately small, close, rather deep punctures, becoming rather shallow laterally and very minutely granulate on lateral rim; a median line obscurely indicated anteriorly. Vestiture scanty, becoming more abundant, longer, and rather coarse anteriorly and laterally.

Elytra 2.3 times as long as pronotum; sides straight and subparallel on basal two-thirds, rather broadly rounded behind; basal margins arcuate and bearing a row of nine, moderately large, raised, overlapping crenulations, with several smaller submarginal ones particularly on interspaces two and three; striae weakly impressed, the punctures rather small and moderately deep; interstriae almost twice as wide as striae and armed by abundant, confused, transverse crenulations, each averaging about two-thirds the width of an interspace, a few wider than an interspace and sometimes crossing striae. Declivity steep, uniformly convex; striae one to three straight, the punctures almost as large as on disc; interstriae one to three about equal in width and bearing rather abundant, somewhat confused (usually arranged in widely staggered single row), moderately large tubercles. Vestiture much longer and more abundant on declivity, a few setae twice as long as width of an interspace.

Female.—Similar in all respects to male except pronotum evidently a little more coarsely punctured and the elytra somewhat more coarsely sculptured.

Type locality.—San Raphael, Mexico, Mexico.

Hosts.—*Pinus leiophylla* and *Pinus* sp.

Distribution.—Central Mexico (Sinaloa) to Guatemala (Fig. 54).

Type material.—The male holotype, female allotype and one paratype were taken at the type locality on September 11, 1949, from *Pinus leiophylla*, by J. P. Perry, Jr., collection no. 49-16028. Five paratypes were taken at Tlalmanalco, Mexico, on January 8 and April 16, 1950, from the same host, by the same collector; two paratypes were taken at Uruapan, Michoacan, Mexico, July 12; one paratype was taken 20 mi. N. E. Copala, Sinaloa, Mexico, by S. L. Wood, from *Pinus;* and eight paratypes are labeled "Guatemala, C. A., *Pinus*, Hopk. U. S. 9929 Gl."

Fig. 54. Probable geographical distribution of *Dendroctonus aztecus* with collection sites indicated (only two of the eight Guatemala records could be verified).

The holotype, allotype and seven paratypes are in my collection; the remaining paratypes are in the California Academy of Sciences and in the U. S. National Museum.

The Guatemala locations marked on the distribution map for this species are listed under *adjunctus*. At least some and possibly all of the series taken in Guatemala included this species: part of the series in question were unavailable for this study.

Geographical variation.—Not observed in the limited material at hand.

Dendroctonus terebrans (Olivier)

Figs. 14, 29, 38, 55.

Scolytus terebrans Olivier, 1795, Entomologie 4(Gen. 78):6.

Dendroctonus terebrans: Erickson, 1836, Archiv f. Naturgesch. 2(1):53; Lacordaire, 1866, Genera des Coleopteres 7:360; Zimmerman, 1868, Trans. American Ent. Soc. 2:149; Leconte, 1868, Trans. American Ent. Soc. 2:173; Chapuis, 1869, Synopsis des Scolytides, p. 35 (reprint of 1873, Mém. Roy. Soc. Sci. Liége, ser. 2, 3:243); Leconte, 1876, Proc. American Philos. Soc.

15:384; Schwarz, 1878, Proc. American Philos. Soc. 17:469; Hopkins, 1906, Proc. Ent. Soc. Washington 7:81; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):147; Provancher, 1877, Fauna Ent. Canada 1:572; Provancher, 1878, Fauna Ent. Canada 1(Add. et Cor.):13, 14; Schwarz, 1886, Ent. Americana 2:56; Schwarz, 1888, Proc. Ent. Soc. Washington 1:80; Dietz, 1890, Trans. American Ent. Soc. 17:28, 29; Blandford 1897, Biol. Centr.-Americana, Coleopt. 4(6):146; Hopkins, 1899, Proc. Ent. Soc. Washington 4:343; Smith, 1900, Cat. Ins. New Jersey, p. 364; Hopkins, 1905, Proc. Ent. Soc. Washington 7:81, 145, 147; Snow, 1907, Trans. Kansas Acad. Sci. 20(2):64; Swaine, 1909, New York St. Mus. Bull. 134:100; Blatchley and Leng, 1916, Rhynchophora or weevils of N. E. America, p. 654; Hagedorn, 1910, Colopterorum Catalogus 4:23; Hagedorn, 1910, Genera Insectorum 111:60; Hopkins, 1915, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(2):211; Beal and Massey, 1945, Duke Univ. School For. Bull. 10:80; Chamberlin, 1939, Bark and timber beetles of North America, p. 167. BIOL.: Thomas, 1876, Nox. Ins. Illinois Rept. 1:146; Smith, 1877, Insects that Infest Shade Trees, etc., p. 55; Packard, 1887, U. S. Dept. Agric. Ent. Comm. Bull. 7:177; Packard, 1890, U. S. Dept. Agric. Ent. Comm. Rept. 5:721, 853; Hopkins, 1893, West Virginia Agric. Expt. Sta. Bull. 31:143, 32:213; Hopkins, 1894, Canadian Ent. 26:280; Hamilton, 1895, Trans. American Ent. Soc. 22:346, 378; Hopkins, 1899, U. S. Dept. Agric. Div. Ent. Bull. 21:27; Hopkins, 1899, West Virginia Agric. Expt. Sta. Bull. 56:392, 415, 421; Chittenden, 1899, U. S. Dept. Agric. Div. For. Bull. 22:56; Lugger, 1899, Minnesota Agric. Expt. Sta. Bull. 66:317; Felt, 1901, Forest, Fish and Game Comm. Rept. 7:480; Hopkins, 1901, U. S. Dept. Agric. Div. Ent. Bull. 28:pl. 12; Smith, 1901, Ent. News 12:92; Felt, 1902, U. S. Dept Agric. Div Ent. Bull. 31:64; Ulke, 1902, Proc. U. S. Natl. Mus. 25:36; Hopkins, 1902, U. S. Dept. Agric. Div. Ent. Bull. 32:10; Hopkins, 1904, U. S. Dept. Agric. Div. Ent. Bull. 48:pl. 7; Felt, 1906, New York St. Mus., Mem. 8, 2:333, 338, 342; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 58:62; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 83(1):146; Blackman, 1922, Mississippi Agric. Expt. Sta. Tech. Bull. 11:56; Felt, 1924, Manual of Tree and Shrub Insects, p. 262; Nelson and Beal, 1929, Phytopath. 19:1102; Craighead et al., 1930, U. S. Dept. Agric. Misc. Pub. 74:4; Craighead, 1935, U. S. Dept. Agric. Misc. Pub. 209:136; Adams, 1937, Arborists News 2(5):3; Friend, 1942, Yale Univ. School For. Bull. 49:145; Felt and Bromley, 1942, Jour. Econ. Ent. 35:170; Felt and Bromley, 1944, Jour. Econ. Ent. 37:213; O'Byrne, 1946, Virginia Agric. Ext. Circ. 403:1, 7; Anderson, 1947, Texas For. Serv. Bull. 33:7; Anonymous, 1951, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv. Sup. 4:8; Beal et al., 1952, Duke Univ. School For. Bull. 14:50; Hoyt, 1952, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1950-51:16; Anonymous, 1952, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Coop. Econ. Ins. Rept. 1(Sup. 4):93; Cross, 1953, South. Lumberm. 187(2336):34; Hoyt, 1953, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1951-52:40; Lee and Smith, 1953, Proc. Assoc. South. Agric. Workers 50:105; Barker and Nettles, 1954, South Carolina Agric. Ext. Circ. 239(rev.):6; Hoyt, 1954, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1952-53:22; Jackson et al., 1954, For. Dis. Ins. Georgia's Trees, p. 26; Smith, 1954, South. Lumberm. 189(2369):155; Smith, 1954, Proc. South. Agric. Workers 51:100; Briegleb, 1955, U. S. Dept. Agric. South. For. Expt. Sta. Rept. 1954:68; Demmon, 1955, U. S. Dept. Agric. S. E. For. Expt. Sta. Rept. 1954:74; Flory et al., 1955, South Carolina Agric. Ext. Bull. 116:8; Lee and Smith, 1955, U. S. Dept. Agric. South. For. Expt. Sta. Res. Notes 76, 2 p.; Ostrow, 1955, Proc. Conf. For. Tree Improv. 3:104; Smith, 1955, Proc. South. Agric. Workers 52:99; Anonymous, 1955, U. S. Dept. Agric. For. Serv. Mor Imp. For. Ins. 1954:14; Bennett, 1955, Texas For. Serv. Circ. 43:2, 8; Bennett, 1956, U. S. Dept. Agric. South. For. Expt. Sta. For. Rptr. 10:10; Briegleb, 1956, U. S. Dept. Agric. South. For. Expt. Sta. Rept. 1955:50; Demon, 1956, U. S. Dept. Agric. S. E. For. Expt. Sta. Rept. 1955:74; Jordan and Dyer, 1956, Georgia Agric. Ext. Circ. 404, 12 p.; Merkel and Kowal, 1956, U. S. Dept. Agric. S. E. For. Expt. Sta. Paper 67:4; Walker, 1956, Georgia For. Res. Counc. Rept. 2:1, 3, 7;

Livingston et al., 1956, Alabama Rept. 64/65:55; Briegleb, 1957, U. S. Dept. Agric. South. For. Expt. Sta. Rept. 1956:67; McCambridge and Kowal, 1957, U. S. Dept. Agric. S. E. For. Expt. Sta. Paper 76:4; Pechanec, 1957, U. S. Dept. Agric. S. E. For. Expt. Sta. Rept. 1956:41; Smith, 1957, Jour. Econ. Ent. 50:241; Smith and Lee, 1957, U. S. Dept. Agric. For. Serv. For. Pest Leaflet 12, 7 p.; Anonymous. 1957, U. S. Dept. Agric. South. For. Expt. Sta. South. For. Rptr. 16:4.

This species is very closely related to *valens*, but is readily distinguished by the black body color, by the much larger punctures on the lateral areas of the pronotum, by the larger, more abundant declivital tubercles, and, in part, by the distribution (Fig. 55).

Male.—Length 5.0-8.0 mm. (average about 6.5), 2.3 times as long as wide; mature body color dark brown to black.

Frons rather evenly convex, with a shallow median impression about a third of distance from upper level of eyes to epistomal margin, very feebly elevated lateral to impression; epistomal margin elelevated, its surface smooth and shining; epistomal process broad, about half as wide (0.50 times) as distance between eyes, its arms oblique (about 30° from the horizontal), elevated only at median angles of arms, the horizontal portion about two-thirds its total width and broadly, transversely concave, overlapping and ending just above epistomal margin and bearing under its distal margin a dense brush of yellowish setae. Vestiture, in addition to epistomal brush, moderately long, sparse, inconspicuous.

Pronotum 1.4 times as wide as long, widest at base; sides weakly arcuate and converging very slightly toward the moderately strong constriction just behind the broadly, shallowly emarginate anterior margin; surface smooth and shining, the punctures moderately large, rather shallow, close, becoming two to three times larger in diameter near lateral margins; bottom or floor of each puncture irregularly reticulate; a partly impunctate, feebly raised median line indicated on posterior two-thirds; vestiture scanty, longer and more evident laterally.

Elytra 2.1 times as long as pronotum; sides straight and subparallel on basal two-thirds, rather broadly rounded behind; basal margins arcuate and bearing a row of about twelve moderately large, raised, overlapping crenulations, with several smaller submarginal ones particularly on interspaces two and three; striae weakly impressed, the punctures small and rather shallow; interstriae more than twice as wide as striae and armed by abundant, confused, transverse crenulations, each averaging about half the width of an interspace, a few about two-thirds as wide on posterior half of disc. Declivity rather steep, convex; strial punctures slightly smaller than on disc; interstrial punctures confused and all rather coarsely granulate, the largest forming a somewhat definite median row on each interspace. Vestiture moderately abundant, longer on declivity, longest setae slightly greater than a distance equal to width of an interspace.

Female.—Similar to male except a median frontal elevation evident at upper level of eyes; epistomal process less well developed; pronotal punctures very slightly larger; and discal crenulations and declivital granules a little larger.

Type locality.—Southern United States (probably Georgia). The concept of this species was based on Hopkins' material; the type was not studied.

Hosts.—*Pinus echinata, elliotti, palustris, rigida, rubens, serotina, strobus,* and *taeda.*

Distribution.—The United States south of a line drawn from New Jersey to eastern Texas.

Specimens from the following localities were examined (Fig. 55). ALABAMA: Aburn, Barton, Calhoun, "DeSoto S. P.," Grand Bay, Mobile and "Redland." ARKANSAS: Hot Springs. DELAWARE: "Delaware." DISTRICT OF COLUMBI(: "Taxoma." FLORIDA: Baker Co., Dunedin, Ft. Lauderdale, Gainesville, "Juniper

Fig. 55. Probable geographical distribution of *Dendroctonus* spp. with collection sites indicated: 1, *valens* (circles); 2, *terebrans* (triangles). Several additional records from southern Mexico and Guatemala have been published for *valens.*

Springs," Largo, Levy Co., Miami, Nassau Co., O'Leno S. P., Opa Locka, Tampa, and Winter Park. GEORGIA: Clayton, Cornelia, Ft. Valley, Kingsland, Myrtle, Thomasville, and Waverly. LOUISIANA: "Hart." MARYLAND: "Baden." NEW JERSEY: Clementon, Iona, "Lahaway," Lakewood, Mt. Misery, and New Brunswick. NEW YORK: Islip, Rockaway Beach and Bay Shore on Long Island. NORTH CAROLINA: Asheville, and Southern Pines. PENNSYLVANIA: Chinchilla. SOUTH CAROLINA: Chicora Place, Lumber, "New Landing," Pregnall, and Spartanburg. TEXAS: Austin, Call, Deweyville, Kirbyville, and Turlington. VIRGINIA: Ashland, "Camp Pickett," Falls Church, "Glen," and King. WEST VIRGINIA: Kanawah Station, Marion Co., Morgantown, Romney, "Roosevelt," and Crow.

Geographical variation.—Distinct differences correlated with geographical origin were not evident.

Biology.—This is a secondary enemy of pines, and less commonly, other coniferous trees; consequently, economic damage attributed to it is slight when compared to some of the other species of *Dendroctonus*.

Since this species has not been observed during the course of this study the following comments are based on personal observations made on two occasions a decade ago, and on the reports of Hopkins (1909b:147) and of Blackman (1922:57).

The principal overwintering stage is the adult, either in the bark of the brood tree or in newly started galleries of another host; they may also pass the winter as partly grown larvae. In the spring the adults became active in March or April and either begin or extend their new galleries as the period of oviposition commences. Overwintering larvae complete their development in the spring and evidently emerge from the brood tree prior to mid-July. The period of flight activity evidently continues more or less gradually from March to December. In the southern parts of its range activity may continue without interruption throughout the year .

Stumps more than four inches in diameter of recently cut trees, or of injured or weakened trees, are selected for attack. Their galleries ordinarily extend downward into the roots; occasionally they extend upward as much as two or three feet above the ground level, except in the southwestern parts of its distribution where they may extend more than 12 feet above the ground (Smith & Lee, 1957:3). Frequently the attacks are made in the vicinity of a wound at the base of the tree. Even though such attacks do not kill the host immediately they may interfere with normal growth, reduce vitality, thereby inviting other insect or disease causing agents to attack the tree.

The attack ordinarily begins at or just above the ground level, usually with only a few pairs of beetles participating. The female constructs the entrance tunnel and normally is joined by the male shortly after she reaches the cambium. If the amount of pitch encountered is excessive the gallery usually is extended upward, otherwise it is extended downward after ascending a centimeter or two. The egg gallery varies considerably in length, but seldom exceeds 30 centimeters. It may be linear, slightly wider than the beetle

making it, or it may be branched; ordinarily it is irregularly widened at various places. As with other species, the male removes the frass from the working area, ejecting it from the entrance hole at first, then later packing it into the unused areas.

There are no individual egg niches. Groups of eggs are deposited rather loosely at one side of the gallery in one of the widened areas. These groups are then separated from the main areas of the gallery by a rather tightly packed partition of frass.

The periods of incubation and of larval development have not been precisely determined. The larvae do not construct individual tunnels, but work together in the phloem tissues in contact with the cambium, extending the cavity started by the parents. In some instances these cavities are said to cover several square feet of the inner bark (Blackman, 1922:58). These extensions by the larvae appear to wander aimlessly, favoring no particular direction. Larvae from eggs laid in the spring evidently pupate by mid-July and emerge in the fall. There is one complete and a partial second generation each year in most areas; two complete generations may occur in the extreme southern parts of its range.

Dendroctonus valens Leconte

Figs. 15-17, 30, 37, 55-56.

Scolytus terebrans: Harris, 1826, New England Farmer 5:169; Harris, 1862, A treatise on Some of the Insects Injurious to Vegetation, p. 56.

Hylurgus terebrans: (Biol.) Harris, 1841, A Report on the Insects of Massachusetts Injurious to vegetation, p. 72; Harris, 1842, A Treatise of Some of the Insects of New England which are Injurious to Vegetation, p. 72, 1852, p. 76; Fitch, 1858, Trans. New York St. Agric. Soc. 18:728; Harris, 1862, A Treatise on Some of the Insects Injurious to Vegetation, p. 86; Harris, 1863, A Treatise on Some of the Insects Injurious to Vegetation, Flint edition, p. 84; Thomas, 1876, Illinois State Entomologist Rept. 6:146; Smith, 1877, *in* Stewart, Shade Trees, Indigenous Shrubs and Vines, p. 52.

Dendroctonus terebrans: Zimmerman, 1868, Trans. American Ent. Soc. 2:149 (in part); Leconte, 1868, Trans. American Ent. Soc. 2:173 (in part); Leconte, 1876, Proc. American Philos. Soc. 15:385 (in part); Provancher, 1877, Faun. Ent. Canada 1:572; Dietz, 1890, Trans. American Ent. Soc. 17:29 (in part); Blandford, 1897, Biol. Centr.-Americana 4(6):146; Hopkins, 1899, Proc. Ent. Soc. Washington 4:343 (in part). Biol.: LeBaron, 1871, Prairie Farmer 42:p.?; Pachard, 1887, U. S. Dept .Agric. Ent. Comm. Bull. 7:175, 243 (in part); Pachard, 1890, U. S. Dept. Agric. Ent. Comm. Rept. 5:721 (in part); Hopkins, 1892, Science 20:64; Hopkins, 1893, West Virginia Agric. Expt. Sta. Bull. 31:143 (in part); Hamilton, 1895, Trans. American Ent. Soc. 22:346, 378; Wickham, 1896, Proc. Davenport Acad. Nat. Sci. 6:169; Wickham, 1896, Bull. Lab. Nat. Hist. State Univ. Iowa 3(4):170; Hopkins, 1897, West Virginia Agric. Expt. Sta. Rept. 6:41; Wickham, 1898, Bull. Lab. Nat. Hist. State Univ. Iowa 6(3):312; Hopkins, 1899, West Virginia Agric. Expt. Sta. Bull. 56:392, 415; Hopkins, 1899, U. S. Dept. Agric. Div. Ent. Bull., n. s., 21:14; Chittenden, 1899, U. S. Dept. Agric. Div. Ent. Bull. 22:56 (in part); Wickham, 1902, Bull. Lab. Nat. Hist. State Univ. Iowa 5(3):309; Felt, 1903, New York St. For. Comm. Rept. 7:480 (in part); Felt, 1906, New York St. Mus., Mem. 8, 2:342 (in part).

Dendroctonus valens Leconte, 1860, Pacific R. R. Explor. 5(2):59; Chapuis, 1869, Synopsis des Scolytides, p. 35 (1873, Mém. Soc. Roy. Sci. Liége

2, 3:243); Powell, 1904, Jour. New York Ent. Soc. 12:237; Powell, 1905, Jour. New York Ent. Soc. 13:5; Hopkins, 1905, U. S. Dept. Agric. Bur. Ent. Bull. 56:6, 11, 17; Hopkins, 1906, Proc. Ent. Soc. Washington 7:147; Hopkins, 1906, Proc. Ent. Soc. Washington 7:81; Swaine, 1909, New York St. Mus. Bull. 134:100; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):151; Hagedorn, 1910, Coleopterorum Catalogus 4:23; Hagedorn, 1910, Genera Insectorum 111:60; Hopkins, 1915, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(2):211 etc.; Blatchley and Leng, 1916, Rhynchophora or weevils of N. E. America, p. 577, 654; Swaine, 1918, Dom. Canada Dept. Agric. Ent. Br. Bull. 14(2):63; Chamberlin, 1939, Bark and Timber Beetles of North America, p. 167; Schedl, 1940 (1939), An. Esc. Nat. Cienc. Biol. 1:320, 323, 339; Schedl, 1955, Zeitschr. Angew. Ent. 38:14; Chamberlin, 1958, Scolytoidea of the Northwest, p. 78. BIOL.: Hopkins, 1902, U. S. Dept. Agric. Div. Ent. Bull. 32:12; Gillette, 1903, Colorado Agric. Rept. 24:118; Hopkins, 1903, Canadian Ent. 35:61; Hopkins, 1904, U. S. Dept. Agric. Div. Ent. Bull. 48:19; Currie, 1905, U. S. Dept. Agric. Div. Ent. Bull. 53:74; Fall, 1907, Trans. American Ent. Soc. 33:218; Burke, 1908, Proc. Ent. Soc. Washington 9:115; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 58:62; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 83(1):153; Hopkins, 1912, U. S. Dept. Agric. Bur. Ent. Circ. 142:6; Swaine, 1913, Ontario Ent. Soc. Rept. 43:90; Swaine, 1914, Dom. Canada Dept. Agric. Expt. Farms. Ent. Bull., ser. 2, 17:20; Compere, 1915, California Hort. Bull. 4:574; Chamberlin, 1917, Canadian Ent. 49:323, 327; Chamberlin, 1918, Oregon Agric. Expt. Sta. Bull. 147:9; Blackman, 1919, Psyche 26:90; Herbert, 1919, Jour. Econ. Ent. 12:337; Hopping, 1921, Canada Dept. Agric. Ent. Br. Circ. 15:12; Hopping, 1922, Canadian Ent. 54:129, 130, 132; Graham, 1922, Minnesota Ent. Rept. 19:15; Blackman, 1922, Mississippi Agric. Expt. Sta. Tech. Bull. 11:22, 28, 58; Felt, 1924, Manual of Tree and Shrub Insects, p. 263; Hatch, 1924, Michigan Acad. Sci. Pap. 6:584; Trimble, 1924, Ann. Ent. Soc. America 17:384; Craighead, 1927, U. S. Dept. Agric. Circ. 411:4; Peirson, 1927, Maine For. Serv. Bull. 5:108, 121; Keen, 1928, California Dept. Nat. Res. Bull. 7:37; St. George, 1929, U. S. Dept. Agric. Farmers Bull. 1586:4; Craighead, 1930, U. S. Dept. Agric. Misc. Pub. 74:4; Blackman, 1931, New York St. Coll. For., Syracuse Univ. Bull. 4(4), Tech. Pub. 36:31; Burke, 1932, California Agric. Mo. Bull. 21:366; Walther, 1933, Jour. Econ. Ent. 26:828; Walther, 1933, Pan-Pac. Ent. 9:47; Kaston, 1936, Connecticut Agric. Expt. Sta. Bull. 387:645; Burke, 1937, Proc. Western Shade Tree Conf. 4:29; Brimley, 1938, North Carolina Dept. Agric. (Insects of North Carolina) :246; Dodge, 1938, Minnesota Agric. Expt. Sta. Tech. Bull. 132:28; Keen, 1938, U. S. Dept. Agric. Misc. Pub. 273:109; Beal, 1939, U. S. Dept. Agric. Farmers Bull. 1824:12; Wheeler, 1940, California Cult. 87:636; DeLeon, 1942, U. S. Dept. Agric. Bur. Ent. Pl. Quar. E-568, 4 p.; Felt and Bromley, 1942, Jour. Econ. Ent. 35:170; Evenden et. al., 1943, U. S. Dept. Agric. Circ. 664; Parr, 1943, Jour. Forestry 41:419; Felt and Bromley, 1944, Jour. Econ. Ent. 37:213; Beal and Massey, 1945, Duke Univ. School For. Bull. 10:81; Leech, 1945, Canada Dept. Agric. Div. Ent. For. Ins. Surv. Rept. 1944:66; Patterson, 1945, Univ. Washington Pub. Biol. 10:150; Anderson, 1947, Texas For. Serv. Bull. 33:7; Bruhn, 1947, Great Basin Nat. 8:21; Weidman nad Robbins, 1947, Jour. Forestry 45:428, 431; Muesebeck, 1950, Jour. Econ. Ent. 43:125, 131; Pearson, 1950, U. S. Dept. Agric. Monogr. 6:154; Craighead, 1950, U. S. Dept. Agric. Misc. Pub. 657:295; Evans and Dyer, 1951, Canada Dept. Agric. Div. Ent. For. Ins. Surv. Rept. 1950:110; Becker, 1951, Zeitschr. angew. Ent. 33:186; Lannon, 1951, Rhode Island Dept. Agric. Cons. Rept. 16:38; Perry, 1951, Unasylva 5:161; Whiteside, 1951, U. S. Dept. Agric. Circ. 864:3; Anonymous, 1951, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest. Surv. Sp. Sup. 4:8; Beal, 1952, Duke Univ. School For. Bull. 14:50; Hoyt, 1952, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1950-51:16; Keen, 1952, U. S. Dept. Agric. Misc. Pub. 275:127, 142; Anonymous, 1952, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Coop. Econ. Ins. Rept. 1(Sup. 4):93; Becker, 1954, Zeitschr. angew. Ent. 36:20; Knight and Wilford, 1954, U. S. Dept. Agric. Rocky Mtn. For.

Range Expt. Sta. Ins. Cond. 1953:4; Reid, 1955, Canadian Ent. 87:316, 323; Shenefelt and Benjamin, 1955, Wisconsin Agric. Ext. Circ. 500:84; Anonymous, 1955, California For. Pest Contr. Action Comm. For. Ins. Cond. 1954:7; Morena Noriega, 1956, Fitofilo 9(15):23, 35; Ostmark and Wilford, U. S. Dept. Agric. Rocky Mtn. For. Range Expt. Sta. Paper 22:6.

Dendroctonus beckeri Thatcher, 1954, Coleopterists Bull. 8:3. BIOL.: Perry, 1955, Coleopterists Bull. 9:1.

This, the largest species in the genus, is very closely related to *terebrans*, but is readily distinguished by the reddish brown body color, by the smaller punctures in the lateral areas of the pronotum, by the smaller, less abundant declivital granules (Fig. 30) and, in part, by the distributions (Fig. 55).

Male.—Length 5.4-9.0 mm. (average about 8), 2.3 times as long as wide; mature body color reddish brown.

Frons irregularly convex, with a pair of lateral protubrances about a third of distance below upper margin of eye to epistomal margin, these protubrances separated by a broad, shallow, subconcave depression; epistomal margin elevated, its surface smooth and shining; epistomal process very broad, equaling about two-thirds (0.60 times) the distance between eyes, its arms oblique (about 20° from the horizontal), elevated only at inner angles of arms, the horizontal portion about two-thirds its total width, broadly concave, overlapping and ending just above epistomal margin and bearing under its distal margin a dense brush of yellowish setae. Vestiture, in addition to epistomal brush, moderately long, sparse, inconspicuous.

Pronotum 1.3 times as wide as long; sides weakly arcuate, almost subparallel, on basal two-thirds then moderately constricted just behind the broadly, shallowly emarginate anterior margin; surface smooth and shining, the punctures very close, rather shallow but sharply impressed, rather small but irregular in size, not larger laterally; an impunctate, feebly raised median line indicated on posterior three-fourths; vestiture scanty, longer and more evident laterally.

Elytra 2.2 times as long as pronotum; sides straight and subparallel on basal two-thirds, rather broadly rounded behind; basal margins arcuate and bearing a row of about twelve moderately large, raised, overlapping crenulations, with several smaller submarginal ones particularly on interspaces two and three; striae weakly impressed, the punctures rather small and deep; interstriae about one and one-half times as wide as striae and armed by abundant, confused, small, transverse crenulations, each averaging about one-third the width of an interspace, almost never more than half as wide on posterior half of disc. Declivity moderately steep, convex, with a feeble impression between first and third striae; strial punctures slightly smaller than on disc; interstrial punctures confused and finely to coarsely granulate, the largest granules forming an indefinite median row (in a few males only this median row of granules appears). Vestiture moderately abundant, longer on de-

clivity, longest setae slightly exceed a distance equal to width of an interspace.

Female.—Similar to male except a median frontal elevation evident at upper level of eyes; pronotal punctures very slightly larger; and discal crenulations and declivital granules a little larger.

Type locality.—California (Totonicapan, Guatemala for *beckeri*). The types of both descriptions were studied. Hopkins did not state that the type of *valens* is a male.

Hosts.—*Pinus arizonica, chicuahuana, contorta, coulteri, echinata, edulis, jeffreyi, lambertiana, lawsoni, leiophylla, monticola, murrayana, oocarpa, ponderosa, pseudostrobus, radiata, resinosa, rigida, rudis, sabiniana, sylvestris, strobiformis, strobus tenuifolia,* and *virginiana, Abies concolor, Larix laricina, Picea canadensis, excelsa,* and *rubens.*

Distribution.—The coniferous forests of America north of Guatemala, except in the extreme southeastern United States.

Specimens from the following localities were examined (Fig. 55). ARIZONA: Apache N. F., Chiricahua Mts., Flagstaff, Ft. Apache Indian Res., Fredonia, Graham Mts., Grand Canyon N. P., McNary, Oak Ck. Canyon, Paradise, Portal, Prescott, Ramsey Canyon, Rincon Mts., Santa Catalina Mts., and Williams. CALIFORNIA: Alder Ck., "Alpine Ck." near Lake Tahoe, Arnold, Bass Lake, Bear Lake, Ben Lomond, Berkeley, Blancos Corral, Boulder Ck., Bray, "Burnt Corral," "BSA Camp" at Oakland, Camp Greenley, Camp Wolfboro, Carmel, Cedar Ridge, Chester, Cisco, Columbia, Cow Ck., Crane Valley, "Crooked Ck.," Crystal Lake, Cummings R. S., "Dark Canyon" in San Jacinto Mts., Del Monte, Devil's Garden, Dorrington, Dunsmuir, "Durley and Herrick Mine" in Plumas Co., Echo Lake, Eldorado, Fallen Leaf Lake, Fresno, General Grant N. P., Hackamore, Halls Flat on Black Mtn., Harvey Valley, Hat Creek, Hayfork, "Hazel Green," Herkey Ck. in San Jacinto Mts., Hobart Mills, Hope Valley, Huckleberry Meadow, Huntington Lake, Idyllwild, Inverness, Jackson, Jacumba, Jamesberg, "Jerome Mill," Julian, Junipero Serra Peak, Kelsey, Lake Co., Lake Arrowhead, Lake Tahoe, Lake Tenaya, "Lake McKenzie," Lamoine, Leavitt Meadows in Lassen Co., Little Yosemite, Lomo, Lone Pine, Loyalton, "Lumgray R. S." Madrone, Manzanita Lake in Lassen N. P., Mather, McCloud, McKenzie, Meadow Valley, Merced, Miami R. S., Milford, Millbrae, Miller Mt. Mill Valley, "Millwood," Mineral, Modoc N. F., Moffitt Ck., Mono Lake, Monterey, Mt. Hamilton, Mt. Hermon, Mt. Laguna, Mt. St. Helena, Nevada City, New Indria, North Fork, Oakland, Old Station, Onion Valley, Oriental, Orinda, Orinda Crossing, Pacific Grove, Palo Alto, Pebble Beach, Piedmont, Pinecrest, Pinehurst, "Pinogrande," Placerville, Plumas N. F., Point Areno, Pollock Pines, Quincy, "Quintette," Rattlesnake Ck., Riverside Co., Sacramento, Salinas, San Bernardino, San Bernardino Mts., "Sand Flat," San Francisco, San Jose, San Mateo, Santa Barbara Co., Santa Cruz, Santa Lucia Mts., Sequoia N. P., Shuteye, Shingle Springs, "Simpson Meadows," Sisson, "Snowline Camp" in Eldorado Co., Solano Co., Stanford, Stauffer, Stewarts Point, Stirling City, "Summerdale," "Sugarloaf Mt." in Los Angeles Co., Tallac, Three Rivers, Timber Mt., Truckee, Viola, Walkermine, Wawona, "Whitaker's Forest in Tulare Co., "Willow Meadow," Willow Ranch, Yreka, and Yuba Gap. COLORADO: Bailey, Cheyenne Mt., Estes Park, Ft. Garland, Douglas Co., Longs Peak, Manitou Park, "Mt. McClellan," Palmer Lake, Placer, "Powder River," Red Mt., San Isabel N. F., and Vallecito R. S. *in* LaPlata Co. IDAHO: Beaver Creek in Logan Canyon, Cedar Mt., Centerville, Coeur d'Alene, Farrogot, Grangeville, Grimes Pass, Harris Ridge, Moscow, Pioneerville, Priest River and Smiths Ferry. ILLINOIS: "Illinois." KANSAS: "Kansas." MAINE: Brunswick, Casco Bay, Limerick, Orono, Paris, Peak Island, and Portland. MASSACHUSETTS: Cambridge, Framingham, Lynn, and Stoneham.

MICHIGAN: Grand Island, and Marquette. MINNESOTA: Aitkin, Cloquet, Duluth, Grand Rapids, Itasca Park, Olmsted, Plummer, Roseau Co., and Two Harbors. MONTANA: Helena, Missoula, and Sula. NEVADA: Reno. NEW HAMPSHIRE: Durham, Manchester, and Webster. NEW JERSEY: Lakehurst, Nilltown, and Newfoundland. NEW MEXICO: "Bright Angel," Capitan, Capitan Mts., Carson N. F., Cloudcroft, Coolidge, "Culdridge," Ft. Wingate, Las Vegas, Lincoln N. F., Ruidoso, Sierra Blanca Mts., and Vermejo. NEW YORK: Hamburg, Ithaca, Syracuse, and West Point. NORTH CAROLINA: Asheville, Balsam, Biltmore, and "Pink Beds." OHIO: Hocking Co. OREGON: Albany, "Anthony Ck.," Ashland, Aspen Lake, Baker, Bourne, Clover Ck., Cold Springs, Colestine, Corvalis, Crater Lake, Hood River, Joseph, Kerby, Klamath Lake, LaGrande, Mt. Hood, Prineville, Pringle Falls, Siskiyou Mts., "Slate Ck.," Sumpter, "Sutton Ck.," and Talent. PENNSYLVANIA: Chambersburg, Milford, and Philadelphia. SOUTH DAKOTA: Black Hills, Custer, Deadwood, Elmore, Lead, and Spearfish. UTAH: Ashley N. F., Escalante, Eureka, Kamas, Logan Canyon, Mammoth Mt., Navajo Mt., and Panguitch Lake. VIRGINIA: Fredericksburg. VERMONT: Fairlee. WASHINGTON: Blewett Pass, Buckeye, Dayton, Easton, East Satsop River, Fairfax, "Grass Prairie," "Half Moon," Malden, Metaline Falls, NewMan, Northport, Olympia, Pullman, Satus Ck., Seattle, Skakomish River, Skakomish, and Toppenish. WEST VIRGINIA: Bretz, Cranesville, Crow, "Deckers Ck.," Hardy Co., Kanawha Station. "Mayfield Hill," Moorefield, Morgantown, Randolph. "Pallslow," Pendleton, Romney, "Roosevelt," and Tucker Mine. WISCONSIN: Ashland, Bayfield, and Madison. WYOMING: "Lynn," Moskee, and Wyoming in Albany Co. ALBERTA: Athabasca Falls, Ft. Chipewyan, and Waterton Lakes N. P. BRITISH COLUMBIA: Aspen Grove, Campbell River, Canford, Kamloops, Little Shuswap Lake, Midday Ck., Nicola, O'Kanagan Landing, Oliver, Peachland, Princeton, "Spious Ck.," Summerland, Trinity Valley, Vernon, Westwold. NORTHWEST TERRITORY: Ft. Smith. NOVA SCOTIA: Kentville. ONTARIO: Ottawa, Prince Edward Co., Toronto, and Quitoico Pk. QUEBEC: Duparquet, Ft. Coulonge, Montreal, Saint Anne, and Saint Johns. BAJA CALIFORNIA: Sierra San Pedro Marlir. CHIHUAHUA: Cerocahui, and Chihuahua. DISTRITO FEDERAL: Mexico. DURANGO: El Salto. HIDALGO: Jacala. MEXICO: Chalco, Ozumba Mt., and Tlalmanalco. MORELOS: Cuernavaca. PUEBLA: Texmelucan. GUATEMALA: Cerro Quemado, Cuchumatenes Mts., El Baul, Guatemala City, Huehuetenanto, La Esperanza, Momostenango, Patzun, Panajachel, Quezaltenango, Totonicapan, and Uruapan.

Geographical variation.—Specimens from the northeastern parts of the range appear to be somewhat smaller than those from other areas; however, this may result from the limited material at hand, rather than actual population difference. The sexual differences of the frons appear to be more strongly developed in series originating in southern Mexico and Guatemala. There is also a tendency for the egg galleries of some specimens from those areas to be elongate and narrow; however, neither the sexual nor the gallery character is found in a majority of the population in those areas.

Biology.—In general, this is a secondary enemy of pine and spruce, but on occasion it attacks and kills apparently healthy trees. It usually works in conjunction with other more aggressive species and, consequently, comparatively little economic loss is attributed to it.

This species may overwinter either as young or mature adults or as partly grown larvae. There is an extreme overlapping of generations which is reflected by the fact that these insects may be seen in flight at any month of the year during their period of activity. In the northern parts of its range this period of activity evidently

is from May to October; in the southern areas the species probably is active throughout the year.

Ordinarily stumps, injured, weakened or dying trees are selected for attack, although in some areas apparently healthy trees are selected. The attack usually is concentrated at or near the ground level at the base of the tree, but in some areas it may extend six or more feet above the level of the ground. Generally this species arrives quite some time after other species have attacked a particular tree.

The attack on any one tree ordinarily involves only a few pair of beetles of this species. It usually begins a few inches above the ground level then progresses above and below that point. It is not concentrated and, in fact, may involve two or more successive generations before the host succumbs.

The egg galleries (Fig. 56) of this species are exceedingly variable. The female, as with other species in the genus, constructs the entrance tunnel. After reaching the cambium region the tunnel extends upward for a short distance. If the amount of pitch encountered is excessive it may continue upward, if not, it may curve

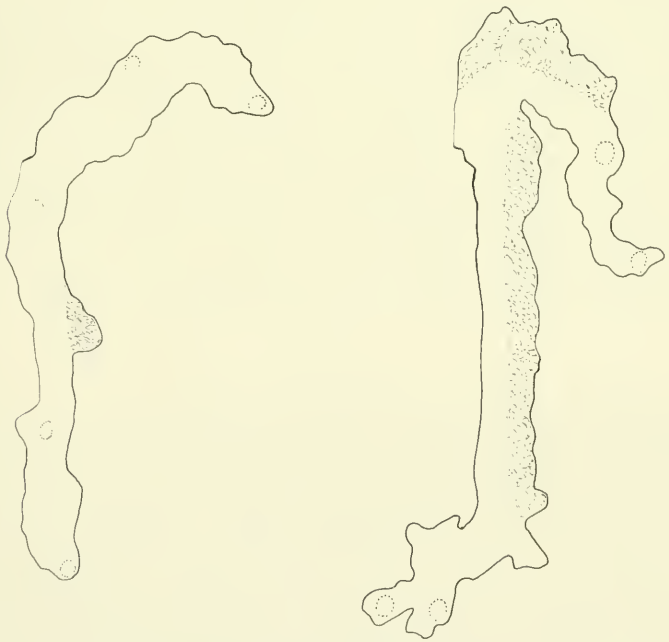

Fig. 56. *Dendroctonus valens*: Egg galleries broad, shape commonly resembling an inverted "J": eggs placed in masses in grooves and packed in frass along sides of galleries (shaded areas above); larvae feed in congress often excavating large tabular areas in the inner bark (larval excavations not included).

downward into the roots. The egg gallery may be linear, slightly wider than the length of the beetle constructing it, or it may be branched or of a broad, irregular cave type. The linear pattern is more common in warmer parts of the range. In southern Mexico egg galleries exceeding 40 centimeters in length were not uncommon; however, it should be mentioned that broad cave-type excavations were found in the same tree with linear galleries as were all degrees of intergradation between the extremes. Usually one side of the gallery is expanded somewhat, either continuously or irregularly, for deposition of the eggs.

Oviposition in most areas of the United States evidently begins in late May or early June and continues throughout the warm months. Egg laying in northern or southern areas probably would begin earlier or later than this. The eggs are deposited along the far side of the expanded parts of the gallery, either loosely packed in frass or in layers, in groups of 10 to 40 or more. They are then covered with a more or less compact layer or partition of frass. There are no egg niches.

According to Swaine (1914:20) the larvae hatch in about ten days. They do not construct individual tunnels but mine in congress in the phloem next to the cambium in a general direction away from the egg gallery. Behind them the large flat cavity is filled by a reddish frass. The length of the larval period has not been determined precisely, but probably exceeds two months; it is suspected that in northern areas it may exceed a year. Pupal cells generally are formed in the frass, although occasionally a larva will construct a short individual tunnel in the phloem adjoining the common cavity where the pupal cell is formed. In the southern parts of its distribution there is one complete and at least a partial second generation each year; in the northern areas a generation evidently may require more than one year.

Dendroctonus micans (Kugelann)

Fig. 21

Bostrichus micans Kugelann, 1794, Schneider Magazin 5:523.

Dendroctonus micans: Erichson, 1836, Archiv Naturgesch. 2(1):53; Eichhoff, 1864, Berliner Ent. Zeitschr. 8:27; Chapuis, 1869, Synopsis des Scolytides, p. 35 (1873, Mém. Soc. Roy. Sci. Liége ser. 2, 3:243); Reitter, 1869, Verh. naturf. Ver. Brünn 8(2):p. ?; Lindemann, 1875, Bull. Soc. Imp. Nat. Moscou 49:213, 221; Lindemann, 1879, Bull. Soc. Imp. Nat. Moscou 54:73; Verhoff, 1896, Archiv Naturgesch. 62(1):124; Lovendal, 1898, De Danske Barkbiller, p. 87; Barbey, 1901, Scolytides l'Europe Centrale, p. 56; Hopkins, 1901, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):143; Hagedorn, 1910, Coleopterorum Catalogus 4:21; Hagedorn, 1910, Genera Insectorum 111:60; Reitter, 1913, Wiener Ent. Zeit. 32(Beiheft):47; Spessivtseff, 1913, (Practical keys to the bark beetles), p. 57; Spessivtseff, 1922, Medd. Skogsförsöksanstalt 19(6):465; Spessivtseff, 1925, Svensk Insektfauna 3:164; Pfeffer, 1932, Cat. Coleopt. Cechosloveniae 2:13; Schedl, 1932, *in* Winkler, Cat. Coleopt. reg. palaercticae, p. 1635; Kurentzov, 1941, Bark-beetles of the Far East, U. S. S. R., p. 116; Balachowsky, 1949, Faune de France 50:134; Stark, 1952, Fauna U. S. S. R., 30:184; Pfeffer, 1955, Fauna C. S. R.

(Czechoslovakia), p. 121. Biol.: Ratzeburg, 1861, Forstl. Bl. 2:64; Heyden, 1874, Jahrb. Nass. Ver. f. Naturk. 27-28:297; Eichhoff, 1880 (1881), Die Europäischen Borkenkäfer, p. 125; Altum, 1881, Forstzoologie 3(1):262; Henschel, 1885, Centralbl. f. d. g. Forsw. 11:534; Heyden, 1887, Ber. ü d. 60 Vers. deutsch. Naturf. u. Aerzte, p. ?; Altum, 1888, Zeitschr. Forst.-Jagdw. 22:242; Judeich and Nitche, 1895, Lehrbuch der mittel europäischen Forstinsektenkunde, p. 458; Severin, 1902, Bull. Soc. Centr. forestière Belg. 9:72, 145; Weber, 1902, Allg. Zeitschr. Ent. 7:108; Brichet and Severin, 1903, Bull. Soc. Centr. forestière Belg. 10:244; Baudisch, 1903, Centralbl. Forstw. 29:151; Bergmüller, 1903, Centralbl. Forstw. 29:252; Bergmüller, 1904, Forstl. Bl., p. 145; Quairière, 1904, Bull. Soc. Centr. Forestière Belg. 11:626; Nüsslin, 1905, Leitfaden der Forstinsektenkunde, p. 175; Quairière, 1905, Bull. Soc. Forstière Belg. 12:183; Quiévy, 1905, Bull. Soc. Centr. Forestière Belg. 12:334; Fuchs, 1906, Zeitschr. Forst.-Landw., p. 291; Formanek, 1907, Kurovci v. Cechach a na Morave zijici, p. 21; Pomerantzew, 1907, Ljaess, Shur. St. Petersburg 37:177; Tredl, 1907, Ent. Blätt. 3:11; Severin, 1908, Bull. Soc. Centr. Forestière Belg. 15:1; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 83(1):141; Koch, 1909, Zeitschr. Forst.-Landw. 7:319; Chabrier, 19—, Mem. Mus. Hist. Nat. 6:470; Saalas, 1913, (reference ?), p. 77; Träghärdt, 1916, Skogsv. Tdjskr., p. 484; Saalas, 1917, Fichtenkäfer Finnlands 2:493; Kneiff, 1923, Mitt. Deutch. Denfrol. Ges., p. 246; Loos, 1925, Sudetendeutsche Forst.-Jagdztg. 25:53; Eulefeld, 1922, D. Forstz. 37:589; Koch, 1928, Bestimmungstabellen Ins. Fichte u. Tanne, p.?; Spessivtseff, 1931, Opredelitel Korojedov, p. 86; Torka, 1933, Ent. Blätt. 29:120; Roubal, 1942, Katalog Coleopt. Slovenska 3:258; Bioltchev, 1934, Lesov. Mis. 3(1):4; Pfeffer, 1943, Lesnická práce 22:181; Karpinski, 1948, Korniky ziem Polski, p. 96; Pfeffer, 1949, Lesnická práce 28:151; Gohrn, 1954, Det. forstl. Forsogsv. i Danmark 21:383.

Hylesinus (*Dendroctonus*) *micans*: Ratzeburg, 1839, Die Forst-Insekten 1:217; Kollar, 1858, Verh. Zool.-Bot. Ges. Wien 7:24; Willkomm, 1863, Thar. f. Jahrb. 15:249; Wahl, 1897, Zeitschr. Forst.-Jagdaw., p. 589; Eckstein, 1904, Zeitschr. Forst.-Jagdw., p. 243; Koch, 1909, Naturw. Zeitschr. Land-Forstw., p. 319.

Hylesinus micans: Geitel, 1862, Verh. Harz. Forstr., p. 21, 1867, p. 13; Gebbers, 1872, Verh. Harz. Forstr., p. 58; Ulrici, 1873, Zeitschr. Forst - Jagdw., p. 150; Glück, 1876, Zeitschr. f. Forst. - Jagdw. 8:385; Pauly, 1892, Zeitschr. Forst. - Jagdw., p. 257, 315, 351; Metzger, 1897, Münd. forstl. Hefte, p. 59; Obertreis, 1897, Zeitscher. Forst - Jagdw., p. 93; Schneider, 1897, Waldungen des Rheinlandes 12:382; F——, 1900, Deutsche Forst. - Zeit. 15:52; Esser, 1901, Wochenschr. Först., p. 286; Eckstein, 1904, Zeitschr. Forst. - Landw., p. 243; Methner, 1935, Wochenbl. Landesb. Pommern 2:216.

This is the only species in the genus occuring outside of the nearctic region. It appears to have reached Eurasia in comparatively recent times and is perhaps doubtfully distinct from the subarctic North American *punctatus*. This species may be distinguished from *punctatus* by the larger size and stouter form, by the flat epistomal process, by the smaller strial punctures, by the somewhat larger elytral crenulations, and by the distribution.

Male.—Length 6.0-8.0 mm. (average about 7), 2.33 times as long as wide; mature body color rather uniformly dark brown.

Frons convex, protruding very slightly in center area just below middle; epistomal margin elevated, smooth, shining; epistomal process a fourth (0.27 times) as wide as distance between eyes, its arms strongly oblique (about 55° from the horizontal) with margins sharply defined but not elevated, the horizontal portion about two-

thirds its total width, flat, overlapping and ending just above epistomal margin and bearing under its distal margin a dense brush of yellowish setae; surface smooth and shining from vertex to epistoma, the punctures rather close, deep, coarse, sharp, with no indication of granules or tubercles. Vestiture fine, long, inconspicuous, rather sparse.

Pronotum 1.4 times as wide as long, widest at base; sides weakly arcuate and converging slightly anteriorly on basal half, then rather abruptly narrowed to a moderate constriction just behind the broadly, shallowly emarginate anterior margin; surface smooth and shining, the punctures rather coarse, close, deep, with a few very minute points interspersed; median line impunctate posteriorly; vestiture moderately abundant, fine and rather short on disc, longer and coarse laterally.

Elytra 2.5 times as long as pronotum; sides straight and subparallel on basal two-thirds, rather broadly rounded behind; basal margins arcuate and bearing a row of about twelve, moderately large, raised, overlapping crenulations, with several smaller submarginal ones particularly on interspaces two and three; striae weakly impressed, the punctures moderately large and deep; interstriae slightly more than twice as wide as striae and armed by abundant confused, small, transverse crenulations, each averaging about one-fourth the width of an interspace, never more than a third as wide on posterior half of disc. Declivity rather steep, convex, with the sutural interspaces slightly elevated; strial punctures almost as large as on disc; interstriae smooth, with numerous confused punctures less than one-third as large as those of striae, about a third of them minutely granulate on upper rim. Vestiture rather long and abundant; slightly longer on declivity, longest setae about one and one-half times as long as width of an interspace.

Female.—Similar to male except frons with a few minute granules between punctures (about one for each six punctures); punctures of pronotum and transverse crenulations of elytra a little larger; and declivital granules much larger.

Type locality.—Europe. The type was not studied.

Hosts.—*Picea excelsea;* less commonly from *Abies*, *Larix* and *Pinus*.

Distribution.—The coniferous forests of northern Eurasia from northern France to Siberia. About 150 specimens representing more than 50 localities were examined.

Geographical variation.—Not evident in the limited material at hand.

Biology.—This is a primary enemy of spruce forests in northern Europe and Asia where extensive damage has been inflicted at various times. Estimates of timber actually destroyed by this insect are not available.

Since the habits and work of this species were not observed

during this study the following was summarized primarily from Eichhoff (1881:125-128) and from Severin (*in* Hopkins, 1909: 142-146).

The winter may be passed either as adults or as partly grown larvae. This indicates that there is an overlapping of generations as in related species. In central Europe the dates of oviposition indicate that the period of flight activity begins late in May or early in June and continues until about August, with the principal period of flight occurring in late June or early July.

Trees selected for attack may be either prostrate or standing; down trees are infested only on the under surface. The lower portion of the bole of standing trees may also be attacked, particularly if the tree is in a weakened condition, although young, vigorous, healthy trees may also be attacked during an epidemic. The pattern of the attack is not clear from available reports, but it is assumed that it progresses upward from the ground level.

The egg galleries tend to be vertical, although they are frequently curved and irregular in shape. They may be up to 20 cm. long, and usually are slightly wider than the beetle making the gallery; ordinarily they have two or three areas expanded on one side or the other. In each of these expanded areas groups of about 20 to 50 eggs are deposited and covered by or separated from the main part of the gallery by a layer or partition of frass. The first eggs are deposited in June and the last ones in September. Evidently one female may re-emerge and construct a second or a third set of galleries.

The larvae feed in congress, forming a large flat cavity in the phloem next to the cambium. There are no egg niches or individual larval mines. The larval period evidently requires at least two months for completion; it commonly continues over winter, pupation taking place during the early part of the following summer. Pupal cells are formed in the frass that fills the larval excavation. There may be one complete and a partial second generation each year.

Dendroctonus punctatus Leconte

Figs. 18, 57.

Dendroctonus punctatus Leconte, 1868, Trans. American Ent. Soc. 2:173; Leconte, 1876, Proc. American Philos. Soc. 15:384, 385; Schwarz, 1886, Ent. Americana 2:56; Hopkins, 1902, Proc. Ent. Soc. Washington 5:3; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):142; Swaine, 1909, New York St. Mus. Bull. 134:98; Hagedorn, 1910, Coleopterorum Catalogus 4:23; Hagedorn, 1910, Genera Insectorum 111:60; Hopkins, 1915, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(2):211; Blatchley and Leng, 1916, Rhyncophora or Weevils of Eastern North America, p. 654; Swaine, 1918, Dom. Canada Dept. Agric. Ent. Br. Bull. 14(2):65. Biol.: Packard, 1887, U. S. Dept. Agric. Ent. Comm. Bull. 7:177; Packard, 1890, U. S. Dept. Agric. Ent. Comm. Rept. 5:722; Hopkins, 1899, West Virginia Agric. Expt. Sta. Bull. 56:447; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. 83(1):139; Felt, 1924, Manual of Tree and Shrub Insects, p. 261.

Dendroctonus rufipennis: Dietz, 1890, Trans. American Ent. Soc. 17:28; Ham-

ilton, 1894, Trans.American Ent. Soc. 21:35; Johnson, 1897, Pennsylvania Dept. Agric. Rept., p. 73.

Dendroctonus johanseni Swaine, 1919, Canadian Arctic Exped. Rept. 1913-1918, 3(E):5 (*new synonymy*); Van Dyke, 1924, Natl. Geographic Soc. Tech. Pap. 2(1):25; Swaine, 1933, Sci. Agric. 14(1):29; Chamberlin, 1939, Bark and Timber Beetles of North America, p. 165.

This species is very closely related to and perhaps doubtfully distinct from the Eurasian *micans*, but may be distinguished by the smaller size, by the more slender form, by the transversely concave epistomal process, by the larger strial punctures, by the smaller elytral crenulations, and by the distributions (Fig. 57). It is more likely to be confused with *murrayanae* and *obesus*, but may be distinguished by the uniformly brown color, by the smooth, polished frons which is deeply punctured but devoid of granules, and by the much larger punctures of the declivital striae.

Male.—Length 5.4-6.8 mm. (average about 6), 2.41 times as long as wide; body color uniformly brown to dark brown.

Frons convex, protruding very slightly at center just below middle; epistomal margin elevated, smooth, shining; epistomal process a third (0.32 times) as wide as distance between eyes, its arms strongly oblique (about 55° from the horizontal) and slightly elevated, the horizontal portion about two-thirds its total width, shallowly concave, overlapping and ending just above epistomal margin and bearing under its distal margin a dense brush of yellowish setae; surface smooth and shining from vertex to epistoma, the punctures rather close, deep, coarse, sharp, interspersed with a few very minute punctures, with no indication of granules or tubercles. Vestiture fine, long, inconspicuous, rather sparse.

Pronotum 1.4 times as wide as long, widest at base; sides weakly arcuate and converging toward the rather strong constriction just behind the broadly, shallowly emarginate anterior margin; surface smooth and shining, the punctures rather fine but irregular, close, deep, with a few very minute points interspersed; median line impunctate posteriorly; vestiture moderately abundant, fine and rather short on disc, longer and coarse laterally.

Elytra 2.5 times as long as pronotum; sides straight and subparallel on basal two-thirds, rather broadly rounded behind; basal margins arcuate and bearing a row of about twelve moderately large, raised, overlapping crenulations, with several smaller marginal ones particularly on interspaces two and three; striae weakly impressed, the punctures large and rather deep; interstriae about one and one-half times as wide as striae and armed by rather abundant confused, small, transverse crenulations, each averaging about one-fourth the width of an interspace, never more than a third as wide on posterior half of disc. Declivity rather steep, convex, with the sutural interspaces slightly elevated; strial punctures almost as large as on disc; interstriae smooth, with numerous confused punctures less than one-third as large as those of striae, about a third of them minutely granulate on their upper rims. Vestiture rather long and

Fig. 57. Probable geographical distribution of *Dendroctonus punctatus* with collection sites indicated.

abundant; slightly longer on declivity, longest setae about one and one-half times as long as width of an interspace.

Female.—So very similar to male that the sexes are recognized only with difficulty; female very slightly more coarsely sculptured, particularly declivital granules very slightly larger.

Type locality.—Northern New York (Sandstone Rapids, Coppermine River, Northwest Territories for *johanseni*). The type of both *johanseni* and *punctatus* were studied.

Hosts.—*Picea glauca, rubens,* and *sitchensis.*

Distribution.—The northern spruce forests from Alaska to New York and south along the mountains to West Virginia.

Specimens from the following localities were examined (Fig. 57). ALASKA: Circle, Haines Rd. (mi. 27), Rampart House, and Savonoski. NEW YORK: "N. Y." PENNSYLVANIA: Mt. Alto. WEST VIRGINIA: Randolph Co. ALBERTA: Cypress Hills, and McKenzie Highway (25th baseline). NORTHWEST TERRITORY: Aklavik, Ft. Smith, and Sandstone Rapids of the Coppermine River. ONTARIO: Fra-

ter. YUKON: Alaska Highway (mi. 1152) Carcross, Carmaks (mi. 8. Mayo Rd.), Rampart House, Watson Lake, Whitehorse, and Wolf Ck.

Geographical variation.—Not observed in the limited material at hand.

Biology.—This species evidently is rare in forests accessible to economic interests; consequently, it is not presently recognized by forest interests as an important species. Structurally and biologically it is so similar to *obesus* that field observers usually do not distinguish it from that species.

It is known to infest the lower bole and stumps of spruce from West Virginia to Alaska. Structurally it is almost indistinguishable from *micans* and is very similar to *murrayanae;* therefore, it is presumed that its biology is equally similar to these species. Collectors who took *punctatus* in two different areas of northern Canada and in Alaska suspected that at least two years were required to complete the life cycle in those areas; one year evidently is sufficient in the Great Lakes area and in the eastern United States.

Dendroctonus murrayanae Hopkins

Figs. 19, 39, 58-59.

Dendroctonus shoshone Hopkins, 1902, Proc. Ent. Soc. Washington 5:3 (*nomen nudum*).

Dendroctonus rufipennis: Hopkins, 1909 (nec. Kirby, 1837), U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):138; Hagedorn, 1910, Coleopterorum Catalogus 4:23; Hagedorn, 1910, Genera Insectorum 111:60; Blatchley and Leng, 1916, Rhyncophora or weevils of Northeastern America, p. 655; Swaine, 1918, Dom. Canada Dept. Agric. Ent. Br. Bull. 14(2):64; Dodge, 1938, Minnesota Agric. Expt. Sta. Tech. Bull. 132:28; Chamberlin, 1939, Bark and Timber Beetles of North America, p. 152. BIOL.: Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 83(1):136; Vitzthum, 1926, Zool. Jahrb. Abt. Syst. Georgr. Tiere 52(5-6):407; Watson, 1931, Canadian Ent. 63:126; Swaine, 1933, Sci. Agric. 14:29.

Dendroctonus murrayanae Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):140; Hagedorn, 1910, Coleopterorum Catalogus 4:22; Hagedorn, 1910, Genera Insectorum 111:60; Swaine, 1918, Dom. Canada Dept. Agric. Ent. Br. Bull. 14(2:64); Chamberlin, 1939, Bark and Timber Beetles of North America, p. 151, 164; Chamberlin, 1958, Scolytoidea of the Northwest, p. 77. BIOL.: Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 83(1): 138; Swaine, 1913, Ontario Ent. Soc. Rept. 43:89; Swaine, 1914, Dom. Canada Dept. Agric. Expt. Farms Bull., ser. 2, 17:28; Hopping, 1922, Canadian Ent. 54:130; Felt, 1924, Manual of Tree and Shrub Insects, p. 261; Craighead, 1927, U. S. Dept. Agric. Circ. 411:9; Keen, 1938, U. S. Dept. Agric. Misc. Pub. 273:109; Clapp, 1942, U. S. Dept. Agric. For. Serv. Rept. 1941:31; Patterson, 1945, Univ. Washington Pub. Biol. 10:150; Watts, 1948, U. S. Dept. Agric. For. Serv. Rept. 1947:27; Reid, 1955, Canadian Ent. 87:316.

This species is very closely allied to *punctatus* and *obesus* and is distinguished from them with considerable difficulty. From *punctatus* it differs by the more closely punctured, sparsely granulate frons (Fig. 19), by the more coarsely punctured pronotum, by the subequal size of strial and interstrial punctures of the declivity, by

the reddish brown elytra with dark brown pronotum, and by the hosts. From *obesus* it differs by the distinctly punctured, finely, more sparsely granulate frons, by the male genitalia (Fig. 39), by the galleries (Fig. 59), and by the hosts.

Male.— Length 5.0-7.3 mm. (average about 6). 2.3 times as long as wide; body color dark brown, with reddish brown elytra.

Frons convex, protruding slightly on lower half; epistomal margin elevated, smooth, shining; epistomal process a third (0.32 times) as wide as distance between eyes, its arms strongly oblique (about 55° from the horizontal) and moderately elevated, the horizontal portion about two-thirds its total width, shallowly concave, overlapping and ending just above epistomal margin and bearing under its distal margin a dense brush of yellowish setae; surface shining from vertex to epistoma, the punctures very close, deep, coarse, about half of them with a small rounded granule on median or lower rim (usually). Vestiture fine, long, inconspicuous, rather sparse.

Pronotum 1.35 times as wide as long, widest at base; sides weakly arcuate and converging toward the rather strong constriction just behind the broadly, shallowly emarginate anterior margin; surface smooth and shining, the punctures rather fine, but irregular, close, deep; median line impunctate posteriorly. Vestiture moderately abundant, fine and rather short on disc, longer and coarse laterally.

Elytra 2.4 times as long as pronotum; sides straight and subparallel on basal two-thirds, rather broadly rounded behind; basal margins arcuate and bearing a row of about twelve moderately large, raised, overlapping crenulations, with several submarginal ones particularly on interspaces two and three; striae very weakly impressed, the punctures rather large and deep, usually decreasing in size toward base; interstriae slightly more than one and one-half times as wide as striae and armed by rather abundant, confused, small, transverse crenulations, each averaging about one-fourth the width of an interspace, never more than a half as wide on posterior half of disc. Declivity rather steep, convex, with the sutural interspaces slightly elevated; striae impressed, the punctures half as large as on disc, usually three times as large as those of interspaces (except in a few examples having unusually large interstrial punctures); interstriae almost smooth, subshining, the punctures rather abundant, confused (very irregularly three-ranked), the median series very finely granulate on upper rims. Vestiture rather long and abundant; slightly longer on declivity, longest setae about one and one-half times as long as width of an interspace.

Female.—Very similar to male except arms of epistomal process less strongly elevated, and declivital granules distinctly larger.

Type locality.—Keystone, Wyoming. The type was studied.

Hosts.—*Pinus banksianna, contorta* and *strobus.*

Distribution.—The Great Lakes area to Alberta, then south to Utah and Colorado.

Specimens from the following localities were examined. COLORADO: Jefferson, Kenosha Pass, and Wheeler Basin. IDAHO: Targhee N. F. MICHIGAN: Grand Island, and Whitefish Point. MINNESOTA: International Falls. MONTANA: Wisdom. UTAH: Logan Canyon and Wolf Ck. Pass. WYOMING: Bighorn Basin, Dubois, "Homestake," Keystone, Saratoga, and Shoshone N. F. ALBERTA: Banff, Cypress Hills, Edmonton, Hillsdale, Jasper N. P., and Lake Louise. BRITISH COLUMBIA: Stanley, and Wycliff. MANITOBA: Clear Lake Trail in Riding Mts. ONTARIO: Black Sturgeon Lake, and Frater.

Fig. 58. Possible geographical distribution of *Dendroctonus murrayanae* with collection sites indicated.

Geographical variation.—Specimens from the Great Lakes area average about 6.1 mm., those from the western half of the distribution about 5.7 mm. Those from the west also tend to have the pronotal punctures and the punctures of the declivital striae and interstriae very slightly larger. These differences are not sufficiently consistent, however, to warrant the recognition of distinct geographic races. It is possible that the apparent geographical differences are invalid, since one short series from Manitoba and another from Black Sturgeon Lake, Ontario, are intermediate in these characters and tend to obliterate any geographical distinctiveness.

Biology.—Ordinarily this is not an aggressive species, although available data indicate that it has contributed to bark beetle epidemics more commonly than published data would suggest and that

it has killed healthy, vigorous Lodgepole pine. Because of the close superficial resemblance to *obesus* some losses actually caused by this species have been attributed to the destructive spruce beetle which supposedly infested Lodgepole pine. In all cases where specimens were preserved for study the "spruce" beetles infesting Lodgepole pine actually were this species.

The overwintering young and old adults and larvae in all stages of development become active when subcortical spring temperatures become sufficiently high, probably about 45° to 50°F. Flight activity probably does not begin before June at the high altitudes in Utah where Lodgepole pine grows. The earliest attacks observed during this study were found in the second week of July. Because of overlapping generations it is suspected that attacks probably continue from late June to early September.

Stumps, windfalls, overmature or weakened trees larger than about eight inches D. B. H. are selected for attack by this species: Trees dying from the attacks of *ponderosae* apparently provide a favorite breeding place for this species. In standing trees the attack seldom extends higher than about two feet above the level of the ground; in addition, it usually extends downward into the roots. In prostrate trees the lower side of the bole is preferred.

The attack evidently begins at or near the ground level at one side of the tree and progresses upward, downward, or around the tree from that point. At times two or more successive generations may be involved in progressively girdling a living tree. Ordinarily only a few pairs of beetles are involved in the attack on a particular tree.

The egg galleries (Fig. 59) are irregularly vertical, slightly wider than the beetle making them, with two or three irregular but shallow expanded areas along one or both sides; often short branch galleries may also be present. The galleries observed during this study averaged about 12 cm. in length; the longest ones were 20 cm. in length; they were constructed entirely by the female. As with other species they were excavated in the phloem in contact with the cambium. In a number of instances it was observed that the female excavated the complete egg gallery before the male appeared; evidently this is not a normal habit. In such instances there were no eggs or larvae in the gallery. When the male was present the lower part of the gallery was packed with frass thereby closing the entrance hole. Copulation was observed twice; in both instances it occurred near the middle of the gallery in one of the expanded areas.

In the Wasatch National Forest in Utah eggs were found during 1960 from July 12 to September 9; it was not determined whether or not these were the first or last eggs of the season. The eggs are deposited in the expanded areas in groups of about 20 to 50 or more. A more or less loose covering or partition of frass separates them from the main parts of the egg gallery. In the galleries observed, from one to three such groups occurred in each gallery.

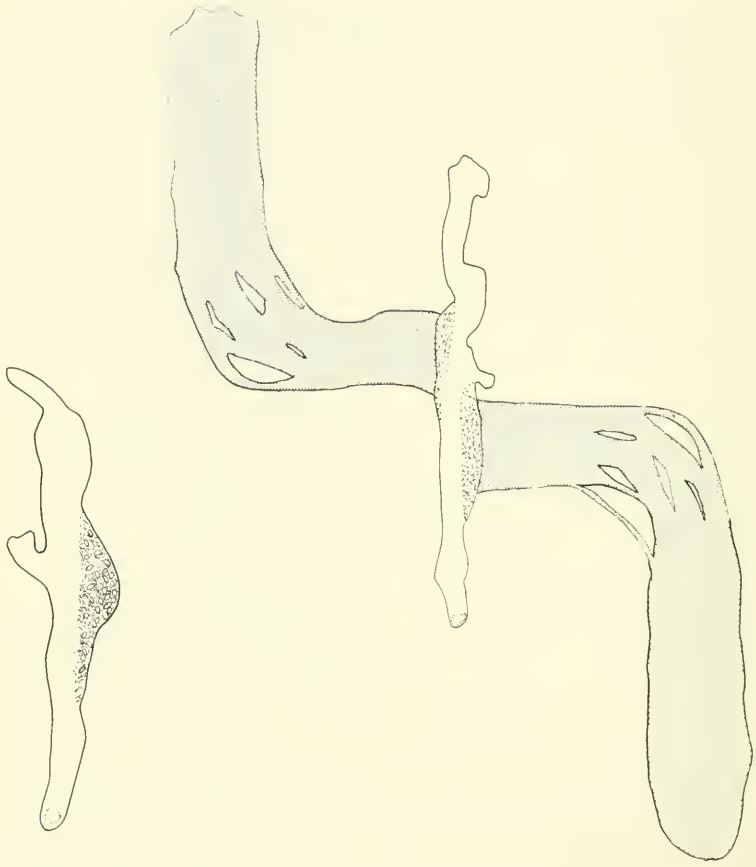

Fig. 59. *Dendroctonus murrayanae*: Egg gallery longitudinal, short, rather irregular; eggs deposited in irregular masses in egg grooves and packed in frass (left); larvae mine in congress, transversely through the second instar, then longitudinally as much as several feet. Characteristically islands of unexcavated bark remain at the angle where the larval mines turn.

Hatching time varied considerably with the season, but probably averaged about ten days in the galleries studied. There were no individual egg niches in any of the galleries. Evidently a female may re-emerge to construct a second set of galleries; this is supported by the fact that in September about a fourth of the galleries studied contained only the female, there were no adults present in an additional fourth.

The larvae feed in congress in a general transverse direction away from the egg gallery (Fig. 59). About six to ten centimeters from the egg gallery the excavated area turns either upward or downward and continues in that direction for an additional 20 to 30 cm. or more. It is characteristic of this species that just before

or just after the vertical turn is made a few small groups of larvae become separated from the main body of larvae and mine independently for short distances before rejoining them. This leaves irregular islands of unexcavated phloem in the general cavity. When near maturity several of the larvae may construct short independent mines where pupation occurs; however, most of the pupal cells occur in the frass of the principal larval excavation. It appeared that the eggs laid in early July were represented by third and fourth instar larvae in September and probably did not mature until the following June; eggs laid in September evidently matured the following July. Evidently there may be one complete and a partial second generation each year in Utah. In the northern parts of the distribution it is possible that less than one complete generation occurs each year.

Dendroctonus obesus (Mannerheim)

Figs. 20, 40, 60-61.

Hylurgus obesus Mannerheim, 1843, Bull. Soc. Imp. Nat. Moscou 16:296; Mannerheim, 1852, Bull. Soc. Imp. Nat. Moscou 25:356; Mannerheim, 1853, Bull. Soc. Imp. Nat. Moscou 26:238.

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This species is very closely allied to *murrayanae* but is distinguished with difficulty by the more coarsely, closely granulate frons (Fig. 20), by the very distinctive male genitalia (Fig 40), by the galleries (Fig. 61), and by the hosts.

Male.—Length 4.4-7.0 mm. (average about 5.5), 2.3 times as long as wide; mature body color very dark brown with reddish brown elytra, old adults usually uniformly black.

Frons convex, protruding slightly on lower half; epistomal margin elevated, smooth, shining; epistomal process a third (0.35 times) as wide as distance between eyes, its arms rather strongly oblique (about 45° from the horizontal) and moderately elevated, the horizontal portion almost two-thirds its total width, shallowly concave, overlapping and ending just above epistomal margin and bearing under its distal margin a dense brush of yellowish setae; surface shining, the punctures very close, deep, rather fine, largely obliterated in central area by fine, abundant granules, at least one or two granules for each puncture in central area, less numerous in surrounding areas. Vestiture fine, long, inconspicuous, rather sparse.

Pronotum 1.4 times as wide as long, widest at base; sides weakly arcuate and converging toward the rather strong constriction just behind the broadly, shallowly emarginate anterior margin; surface smooth and shining, the punctures rather fine but irregular in size, close, deep; median line impunctate posteriorly. Vestiture moderately abundant, fine and rather short on disc, longer and coarse laterally.

Elytra 2.4 times as long as pronotum; sides straight and subparallel on basal two-thirds, rather broadly rounded behind; basal margins arcuate and bearing a row of about twelve moderately large, raised, overlapping crenulations, with several smaller submarginal ones particularly on interspaces two and three; striae very weakly impressed, the punctures rather large and shallow, usually decreasing slightly in size toward base; interstriae slightly more than one and one-half times as wide as striae and armed by rather abundant confused, small, transverse crenulations, each averaging about one-fourth the width of an interspace, never more than a third as wide on posterior half of disc. Declivity rather steep, con-

vex, with the sutural interspaces slightly elevated; striae usually not impressed. the punctures minute, subequal in size to and often confused with those of interspaces; interstriae almost smooth, subshining, the punctures rather numerous, confused, the median series on each interspace very minutely granulate on upper rims. Vestiture rather long and abundant; slightly longer on declivity, longest setae about one and one-half times as long as width of an interspace.

Female.—Very similar to male except arms of epistomal process less strongly elevated, and declivital striae usually weakly impressed with the interstrial granules rather large and usually pointed.

Type locality.—Sitka Island, Alaska (Boreal North America for *rufipennis;* Oregon for *similis;* Camp Caribou, Maine, for *piceaperda;* Eagle, Alaska, for *borealis;* and Capitan, New Mexico, for *engelmanni*). All six types were studied.

Hosts.—All species of *Picea* within its range.

Distribution.—The spruce forests of North America from Alaska to Nova Scotia, south to Pennsylvania in the east and to the Mexican border in Arizona and New Mexico in the west.

Specimens from the following localities were examined (Fig. 60) ALASKA: Chichagof Isl., Circle, Eagle, Eklutna, Ft. Yukon, Homer, Juneau, Kenai Peninsula, Klutina Lake, Matanuska, Nutzotin Mts., Ruby, St. James Bay, Savonoski, Seward, Skaway, Tanana, and Yakutat. ARIZONA: Chiricahua Mts., San Francisco Peak. CALIFORNIA: Crescent City. COLORADO: Argentine Pass, Boulder, Clyde, Ft. Collins, Glenwood Springs, Gore Pass, Gunnison, Hahns Peak, Holy Cross Mtn., Leadville, "Leavenworth Valley," Meeker, New Castle, Ouray Peak, Pingree Pk., Rabbit Ears Pass, San Isabel N. F., Silver Plume, Steamboat Springs, "Twinn Sisters," and White River N. F. IDAHO: Beaver Ck. of Logan Canyon, Collins, and Lieber Ck. in Coeur d'Alene N. F. MAINE: Beaver Pond, Camp Caribou, Cupsuptic, and "Meadows." MICHIGAN: Grand Island, Isle Royal, Marquette, and Munising. NEW HAMPSHIRE: Colebrook, West Stewartstown, and Wonalancet. MINNESOTA: Itasco St. Pk., and International Falls. NEW MEXICO: Capitan Mts., Cloudcroft, Las Vegas, Pecos Wilderness Area, Sandia Mts., Santa Fe Basin, and Sierra Blanca Mts. NEW YORK: Pleasant *Lake.* OREGON: Batterson, Cannon Beach, Cascade Head Expt. For., Coos Bay, Gold Lake, "Highland Mine," Hood River Meadows, Joseph, Marshfield, "Mt. Misery," Mt. Ashland, Santiam Pass, and Tolgate. PENNSYLVANIAS Ricketts. SOUTH DAKOTA: Black Hills N. F., and Spearfish Canyon. UTAH: Alta, Ashley N. F., Cedar Breaks N. M., Ephraim, Escalante, LaSal Mts., Logan Canyon, Lost Lake, Panguitch, Paradise Pk., Parowan Canyon, and Wolf Ck. Pass. WASHINGTON: Aberdeen, Easton, Fairfax, Hoquiam, Lake Wenatchee, Metaline Falls, Morse Ck., Mt. Rainier, Neah Bay, Parkway, Sappho, "Tieton R. S.," Wenatchee Lake, White Pass, White River, Winthrop, and Yakima. ALBERTA: Babine Lake, Banff, Calgary, Cypress Hills, Edmonton, Exshaw, Harlech, Jasper N. P., Kananskis For. Sta., Lake Athabasca, Lake Louise, Lesser Slave Lake, Nordagg, and Smoky Lake. BRITISH COLUMBIA: Aspen Grove, Babine Lake, Bloom Ck. Valley, Boundary Lake, Creighton Valley, Emerald Lake, Glacier, Lorna, Lower Post, Lumberton, Lumby, Ootsa Lake, "Paxton Valley," Priest River, Princeton, Queen Charlotte Islands, Salmo, "Seymour Ck.," Stanley, Trinity Valley, Vancouver, Vernon, Vermilion Summit on Banff Rd., Victoria, Ymir, and Yoho N. P. MANITOBA: Churchill, "Northern Manitoba," and Riding Mt. N. P. NEW BRUNSWICK: Nictor Lake and Fredericton. SASKATCHEWAN: "Northern Saskatchewan." NORTHWEST TERRITORY: Aklavik, Coppermine River, Ft. Norman, Ft. Smith, and Yellowknife. NOVA SCOTIA: Cape Breton Isl., and St.

Fig. 60. Probable geographical distribution of *Dendroctonus obesus* with collection sites indicated.

Peters. ONTARIO: Black Sturgeon Lake, Egg Lake in Algonquin Pk., Frater, Hearst, "Nighthawk Lake," North Bay, "Remi Lake," and Timmins. QUEBEC: Anticosti Isl., Cascapedia, Duparquet, and Gaspe Peninsula. YUKON: Teslin and Whitehorse.

Geographical variation.—Specimens from the eastern part of the distribution average about 0.2 mm. smaller than those from the west. A higher percentage of western specimens, particularly from Sitka spruce in British Columbia, are black in color (38 per cent); only an occasional eastern specimen was black. Whether this was due to the age of specimens at the time of collection, to climatic or other environmental factors, or to genetic factors is uncertain.

Biology.—This is the most destructive of the spruce inhabiting bark beetles. It is responsible for killing an estimated average of approximately one-third to one-half billion board feet of standing spruce timber each year. It is also reported to have inflicted substantial losses to Lodgepole Pine (Massey and Wygant, 1954:1), but this was not substantiated by an examination of the beetles collected from the infested pine trees (cf. *murrayanae*).

The spruce beetle may overwinter in any stage of development, but adults and half grown larvae predominate. Activity evidently begins in May when subcortical daytime temperatures reach about 45° to 50°F. The period of flight activity evidently begins late in May and continues until October, with two distinct seasonal peaks. The first of these is in June, and the second in late July to early September. Local climatic conditions or peculiarities of a particular season may accelerate or delay these peak periods a week or two and may also have a bearing on which of the two flight periods is greater. The first flight includes overwintered parent and young adults, the second primarily consists of beetles that mature from overwintered larvae.

Under endemic conditions the trees selected for attack consist of windfalls or other prostrate dying green trees or of overmature or weakened standing trees larger than about eight inches D.B.H. During an epidemic almost any spruce tree in the stand may be selected regardless of size or vigor. The attack usually begins on the lower third of the bole, except for the first two or three feet above the ground. It ordinarily progresses to include the upper bole and stump later in the season when the second flight occurs, if populations are not excessive. In prostrate trees only the lower half next to the ground is attacked. The upper bole smaller than eight inches in diameter and limbs generally are not subject to attack by this species. The attack is slow and continuous, without any sudden or concerted swarming of the beetles; its duration may vary from a few days to many months, depending on the population density of beetles in the area, upon the resistance of the host, or upon climatic or other ecological factors peculiar to the season or locality. The number of attacks per square foot of bark surface may be as high as 24, but averages between six and nine; the density of the attacks evidently is greater at the base of the tree and gradually decreases upward (Massey and Wygant, 1954:13).

The egg galleries (Fig. 61) are constructed by the female beetle mostly in the phloem tissues, but they engrave the wood more deeply than other species of *Dendroctonus*: the thinness of spruce bark may have some bearing on this habit. The egg galleries are vertical, almost straight, ordinarily with the lower one or two centimeters next to the entrance hole hooked diagonally to either the right or left. The average length of 13 cm. and the maximum length of 23 cm. for egg galleries observed during this study, made in 1960, in the Wasatch National Forest of Utah, agrees with that reported by Massey and Wygant (1954:13). The egg galleries are slightly wider than the width of the beetle making them and, in addition, there usually is an egg groove along the side next to the cambium about one or two millimeters deep. Ventilation tunnels are placed at irregular intervals, but are not always present.

Oviposition evidently begins less than a week after the attack; there is some question as to its duration because most of the beetles re-emerge to construct a second or third set of galleries. Massey

Fig. 61. *Dendroctonus obesus*: Egg gallery longitudinal, rather short; eggs deposited in irregular single or double rows in grooves (occasionally in individual niches as shown at upper left): larval mines usually independent through first instar, usually communal during second and sometimes third instars, usually independent but frequently crossing one another through final stages.

and Wygant (1954:15) reported a maximum of 144 eggs in one gallery; they also reported that there was an average of 20.5 eggs per inch of gallery (excluding the diagonal first inch). In the present study it was found that the number of eggs per inch of gallery where eggs occurred was equal to that found by Massey and Wygant, but this rate of deposition was seldom maintained for more than a third the length of the gallery. The largest number of eggs counted in one gallery during this study was 53 in an area where a small epidemic was beginning on the Wasatch National Forest.

There is considerable variation in the way eggs are deposited. In some galleries all or part of the eggs are placed individually in separate niches. These niches may be lengthened sufficiently to accommodate two or more eggs, or extended into elongate grooves as much as eight centimeters in length. The niches, or the more typ-

ical grooves, ordinarily are placed alternately on the sides of the egg tunnel in contact with the cambium. Ordinarily, individual niches are formed when the gallery enters a moderately unfavorable environment. Each egg or group of eggs is covered by a layer or partition of frass that separates them from the main gallery.

Following oviposition the gallery may be extended a short distance in an irregular feeding tunnel. When both parents are represented separate feeding tunnels may give the gallery a characteristic Y-shaped ending. Evidently most of the beetles re-emerge to form a second or third set of galleries.

At the high altitudes where this species occurs in Colorado incubation is thought to require three to four weeks (Massey and Wygant, 1954:16); it probably takes much less time in Pacific Coast areas where suitable hosts enable this species to live at or near sea level. The newly hatched larvae feed in the phloem in contact with the cambium, either individually or in groups, in a general direction at right angles away from the egg gallery. Ordinarily communal feeding is the rule during the second instar (Fig. 61). When about one-third grown all larvae form separate feeding tunnels that wind throughout the phloem frequently crossing one another. Some larvae that hatch from the first eggs deposited in June may become callow adults by October, however most of them overwinter as larvae and complete their development the following spring. Pupal cells are formed at the ends of the larval mines or in frass of a previously excavated area, either next to the cambium or entirely in the bark. The pupal period in the late spring or early summer may be completed in about 10 to 15 days (Massey and Wygant, 1954:17), however completion of this stage may take several months if pupation begins in the late fall and continues through the winter. A normal life cycle evidently requires from one to two years.

The low temperatures which prevail throughout much of the year in many areas where this species occurs may have a profound effect on the length of the life cycle of this insect. Collectors who took it in the McKenzie River area in northern Canada and in northcentral Alaska estimated that at least two years were required for larval development. The most remarkable adjustment this species has made to survive low temperatures, however, was reported by Massey and Wygant (1954:8) from studies conducted in Colorado. Many of the beetles emerged from brood galleries and went to the bases of trees, ordinarily a brood tree, where they reentered the host at or near the ground level. Here they passed the winter in feeding tunnels, then re-emerged in June or July to begin a new attack. It was estimated that about half of the beetles passed the winter in the same spot where they became adults; the remaining half included those beetles with the special overwintering habit. This hibernation habit has not been reported from other parts of the distribution of this species, nor has it been reported for any other species of *Dendroctonus;* almost certainly it is not restricted to the Colorado area, nor to this one species.

Dendroctonus simplex Leconte

Figs. 22, 41, 62.

Dendroctonus simplex Leconte, 1868, Trans. American Ent. Soc. 2:173; Leconte, 1876, Proc. American Philos. Soc. 15:384, 385; Provancher, 1878, Fauna Ent. Canada 5(Add. et Cor.):13, 14; Schwarz, 1886, Ent. Americana 2:56; Schwarz, 1888, Ins. Life 1:162; Dietz, 1890, Trans. American Ent. Soc. 17:28, 31; Hopkins, 1898, U. S. Dept. Agric. Div. Ent. Bull. 17:69; Hopkins, 1899, Proc. Ent. Soc. Washington 4:343; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):117; Swaine, 1909, New York St. Mus. Bull. 134:99; Hagedorn, 1910, Coleopterorum Catalogus 4:23; Hagedorn, 1910, Genera Insectorum 111:60; Blatchley and Leng, 1916, Rhynchophora or weevils of Eastern America, p. 653; Swaine, 1918, Dom. Canada Dept. Agric. Ent. Br. Bull. 14(2):62; Chamberlin, 1939, Bark and Timber Beetles of North America, p. 152, 162. Biol.: Packard, 1887, U. S. Dept. Agric. Ent. Comm. Bull. 7:177; Packard, 1890, U. S. Dept. Agric. Ent. Comm. Rept. 5:722; Harrington, 1891, Canadian Ent. 23:27; Hopkins, 1898, Proc. Soc. Prom. Agric. Sci. 19:104; Hopkins, 1899, West Virginia Agric. Expt. Sta. Bull. 56:392, 394; Felt, 1906, New York St. Mus., Mem. 8, 2:752; Fall and Cockerell, 1907, Trans. American Ent. Soc. 33:218; Hopkins, 1907, U. S. Dept. Agric Yearbook 1906:515; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 83(1):103; Swaine, 1913, Ontario Ent. Soc. Rept. 43:89; Hewitt, 1917, Canada Dept. Agric. Ent. Br. Rept. 1916:36; Blackman and Stage, 1918, New York St. Coll. For., Syracuse Univ. 4(4), Tech. Pub. 10:39; Felt, 1924, Manual of Tree and Shrub Insects, p. 261; Peirson, 1929, Maine or. Serv. Bull. 5:79; Simpson, 1929, Canadian Ent. 61:274; Prebble, 1933, Canadian Ent. 65:145; Dodge, 1938, Minnesota Agric. Expt. Sta. Tech. Bull. 132:27; Weber, 1942, Minnesota Dept. Conserv., Statis Rept. 1941:79; McGuffin and Barker, 1947, Canada Dept. Agric. For. Ins. Surv. Rept. 1946:57; Anonymous, 1955, U. S. Dept. Agric. For. Serv. Imp. For. Ins. 1954:18.

The only species closely allied to this species is *pseudotsugae* from which *simplex* is distinguished by the much smaller size, by the less strongly protubrant, smoother but more coarsely punctured frons (Fig. 22), by the more coarsely punctured pronotum, by the larger punctures on the declivital interspaces, and by the distribution (Fig. 62).

Male.—Length 3.4-5.0 mm. (average about 4.2), 2.4 times as long as wide; mature body color dark brown, elytra often with a reddish cast.

Frons broadly convex, protruding somewhat on lower half, the inflated area arising abruptly just above the smooth, elevated rim of epistomal margin; epistomal process less than a third (0.30 times) as wide as distance between eyes, its arms very strongly oblique (about 80° from the horizontal) and usually not elevated, the horizontal portion about three-fourths its total width, flat, overlapping and apparently flush with epistomal margin (actually ending just above the slightly extended margin) and bearing under its distal margin a dense brush of yellowish setae; surface shining, smooth, with rather coarse, deep, very close punctures and a very few minute granules. Vestiture sparse, rather short, fine, inconspicuous.

Pronotum 1.4 times as wide as long; widest at base, sides weakly arcuate and converging toward the rather strong constriction just

behind the broadly, shallowly emarginate anterior margin; surface smooth and shining, the punctures rather coarse, irregular in size, close, deep; median line narrowly impunctate posteriorly. Vestiture moderately abundant, fine and rather short on disc, longer and coarse laterally.

Elytra 2.5 times as long as pronotum; sides straight and subparallel on basal two-thirds, rather broadly rounded behind; basal margins arcuate and bearing a row of about ten rather large, raised, overlapping crenulations, with several smaller submarginal ones particularly on interspaces two and three; striae weakly impressed, the punctures rather large and deep, usually decreasing slightly in size toward base; interstriae less than one and one-half times as wide as striae and armed by an irregular row of transverse crenulations, each averaging about one-third the width of an interspace, a few half as wide on posterior half of disc, a few fine punctures interspersed with crenulations. Declivity rather steep, convex, with sutural interspace very strongly elevated and interspace two weakly impressed; striae rather deeply, narrowly impressed, the punctures greatly reduced; interstrial punctures rather coarse, numerous and confused on one, uniseriate on two and three; none of the punctures granulate. Vestiture rather coarse, slightly longer on declivity, the longest setae equal in length to about one and one-half times the width of an interspace.

Female.—Very similar to male except declivital interspaces with minute confused punctures and each with a median row of coarse, somewhat pointed tubercles, the tubercles spaced by a distance slightly less than width of an interspace.

Type locality.—Canada. The type was studied.

Hosts.—Larix laricina.

Distribution.—The eastern United States and Canada north of West Virginia west to northern British Columbia and Alaska.

Specimens from the following localities were examined (Fig. 62). ALASKA: College, Fairbanks, and McGrath. MAINE: Cupsuptic. MICHIGAN: East Lansing, Grand Island, Grand Ledge, Mackinac Isl., Marquette, Munising, Port Huron, and Seney. MINNESOTA: Carlton Co., Hennepin Co., Itasca St. Pk., Lake Itasca, Mille Lacs Co., Pine River, and St. Paul. NEW HAMPSHIRE: Pittsburg, and West Stewartstown. NEW YORK: Erie Co. WEST VIRGINIA: Cranesville. ALBERTA: Bilby, Edmonton, Mitsue, and Smith. BRITISH COLUMBIA: Wildmare Ck. NEW BRUNSWICK: Fredericton, and Nictor Lake. NEWFOUNDLAND: "Newfoundland." NOVA SCOTIA: Sydney. ONTARIO: Deili, Pine Springs, and Wooler. QUEBEC: Gaspe, Natashquan, and Ungara Bay.

Geographical variation.—Not evident in the material at hand.

Biology.—This species prefers dying or injured trees, and consequently, is not generally regarded as having major economic importance. However, it is known to have successfully attacked and killed healthy mature larch trees.

This species was not observed during this study; all comments which follow are based on Hopkins (1909b:103-106), Simpson

Fig. 62. Probable distribution of *Dendroctonus* spp. with collection sites indicated: 1, *pseudotsugae* (circles); 2. *simplex* (triangles).

(1929:274-279) and Prebble (1933:146). The galleries illustrated by Hopkins for this species are used as the basis for the qualified description of the galleries below. Since the placement of eggs in his figure lack detail, since the system appears to resemble that of the very closely related *pseudotsugae*, and because of the general phyletic position of *simplex* in the genus, it is presumed that egg grooves, not niches as illustrated, would normally be constructed by this species.

The principal overwintering stage is the young adult in the brood gallery, although it is not uncommon for some larvae to overwinter. Flight activity begins early in May and continues at a relatively low level until late August; the period of greatest activity apparently is from the last week of May to the second week of June. Adult beetles may re-emerge to construct a second or third set of galleries during the season, but none of their progeny leave the brood tree until the following spring.

Trees selected for attack include windfalls, snow breaks, stumps or other weakened or severely damaged material. The exact pattern

of the attack and details of the galleries and habits have not been reported.

Hopkins (1909b:103) indicated that the galleries are vertical and slightly sinuate. Evidently they average about 20 to 25 cm. in in length. The eggs are deposited in groups of three to six or more, presumably in grooves rather than in individual niches. The larvae mine individually in continual contact with the cambium away from the egg gallery and without crossing one another. Evidently the larval mine increases only slightly through the first and second instars then expands suddenly into an irregularly oval feeding area where the last two larval instars, pupation and hibernation occur.

Oviposition ordinarily begins about the last week of May. The eggs hatch in about 11 days (Prebble, 1933:146) and complete larval development in approximately 27 days; about seven days are required for the pupal stage during the early summer months. Simpson found young adults in the first set of galleries completed during the season by August 1; in the second set of galleries young adults were present by September 17; larvae produced in the third set of galleries formed by these same parent adults passed the winter as larvae. The young adults produced in the first and second sets of galleries overwintered in those galleries and emerged the following May and early June. The overwintered larvae from the third set of galleries matured in June and emerged during July.

Dendroctonus pseudotsugae Hopkins

Figs. 23, 42, 62-63.

Dendroctonus similis: Leconte, 1876, Proc. American Philos. Soc. 15:385 (in part); Leconte, 1878, Bull. U. S. Geol. Geogr. Surv. 4:469; Packard, 1887, U. S. Dept. Agric. Ent. Comm. Bull. 7:177; Packard, 1890, U. S. Dept. Agric. Ent. Comm. Rept. 5:722; Dietz, 1890, Trans. American Ent. Soc. 17:30; Hopkins, 1899, West Virginia Agric. Expt. Sta. Bull. 56:392; Hopkins, 1899, U. S. Dept. Agric. Div. Ent. 21:10, 11, 21, 22, 26; Wickham, 1902, Bull. Lab. Nat. Hist. St. Univ. Iowa 5:310; Fall, 1907, Trans. American Ent. Soc. 33:218.

Dendroctonus pseudotsugae Hopkins, 1901, Proc. Soc. Prom. Agric. Sci. 22:67 (*nomen nudum*); Hopkins, 1903, Canadian Ent. 35:60; Hopkins, 1904, U. S. Dept. Agric. Div. Ent. Bull. 48:19, 45 (*nomen nudum*); Hopkins, 1905, U. S. Dept. Agric. Bur. Ent. Bull. 56:10, 11; Hopkins, 1906, Proc. Ent. Soc. Washington 8:4; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):121; Hagedorn, 1910, Coleopterorum Catalogus 4:22; Hagedorn, 1910, Genera Insectorum 111:60; Swaine, 1918, Dom. Canada Dept. Agric. Ent. Br. Bull. 14(2):62; Chamberlin, 1939, Bark and Timber Beetles of North America, p. 150, 159; Chamberlin, 1958, Scolytoidea of the Northwest, p. 73. BIOL.: Swaine, 1914, Dom. Canada Dept. Agric. Ent. Br. Bull. 7:28; Brunner, 1915, U. S. Dept. Agric. Bull. 255:5; Chamberlin, 1917, Canadian Ent. 49:324; Chamberlin, 1918, Oregon Agric. Expt. Sta. Bull. 147:17; Hopping, 1921, Dom. Canada Dept. Agric. Circ. 15:10; Hopping, 1922, Canadian Ent. 54:131; Gibson, 1923, Canada Dept. Agric. Ent. Br. Rept. 1919-20:16; Felt, 1924, Manual of Tree and Shrub Insects, p. 258; Hofmann, 1924, U. S. Dept. Agric. Bull. 1200:53; Caverhill, 1925, British Columbia Dept. Lands For. Rept. 1924:E-17; Craighead, 1927, U. S. Dept. Agric. Circ. 411:11; Craighead, 1930, U. S. Dept. Agric. Misc. Pub. 74:5; Craighead, 1931, Jour. Forestry 31:1016; Hopping, 1932, Timberman

33(7):61; Bedard, 1933, Jour. Econ. Ent. 26:1128; Beal, 1935, Timberman 37(2):14; Furniss, 1936, Timberman 37(3):21; Furniss, 1937, Timberman 39(2):11; Bedard, 1937, Washington St. Coll. Res. Studies 5:103; Hopping, 1939, *in Mulholland*, Forest Resources of British Columbia, p. 62; Keen, 1938, U. S. Dept. Agric. Misc. Pub. 273:119; Beal, 1939, Rocky Mtn. Conf. Ent. Rept. 15:6; Furniss, 1941, U. S. Dept. Agric. For. Serv. Fire Contr. Notes 5:211; Hopping, 1942, Canadian Ent. 74:205; Kimmey and Furniss, 1943, U. S. Dept. Agric. Tech. Bull. 851:20; Patterson, 1945, Univ. Washington Pub. Biol. 10:149; Hopping, 1947, Canadian Ent. 79:150; Leech, 1947, Canada Dept. Agric. For. Ins. Surv. Rept. 1946:80; Leech, 1947, Canada Dept. Agric. Ins. Pest Rev. 25:63; Anonymous, 1947, California Dept. Nat. Res. Div. For. For. Ins. Cond. 1946:10; Mahaffay, 1948, American For. 54:64, 80; Anonymous, 1948, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv. 1947:17; MacKay, 1948, Canada Dept. Agric. For. Ins. Surv. Rept. 197:94; MacKay, 1949, Canada Dept. Agric. For. Ins. Surv. Rept. 1948:114; Bedard, 1950, U. S. Dept. Agric. Circ. 817, 10 p.; Evans, 1950, Canada Dept. Agric. For. Ins. Surv. Rept. 1949:106; MacKay, 1950, Canada Dept. Agric. For. Ins. Surv. Rept. 1949:114, 120; Anonymous, 1950, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv. 1949:26; Anonymous, 1950, U. S. Dept. Agric. Pacific Northw. For. Range Expt. Sta. Rept. 1949:52; Beal, 1951, Proc. West. For. Conserv. Assoc. 41:58; Evans and Dyer, 1951, Canada Dept. Agric. For. Ins. Surv. Rept. 1950:110; Kenney, 1951, British Columbia Dept. Lands For. For. Serv. Rept. 1950:63; Richmond and Kinghorn, 1951, For. Chron. 27:31; Ross and Jones, 1951, Canada Dept. Agric. For. Ins. Surv. Rept. 1950:114; Anonymous, 1951, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv. Sp. Sup. 4:7; Anonymous, 1951, U. S. Dept. Agric. Bur. Ent. Pl Quar. Ins. Pest Surv. 1950:25; Evans and Dyer, 1952, Canada Dept. Agric. For. Ins. Surv. Rept. 1951:108; Graham, 1952, British Columbia Lumberm. 36(7):52; Anonymous, 1952, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Coop. Econ. Ins. Rept. 1(Sp. Rept.):92; Evans and Dyer, 1953, Canada Dept. Agric. For. Ins. Surv. Rept. 1952:130; Richmond, 1953, British Columbia Dept. Lands For. For. Serv. Rept. 1952:86; Richmond, 1953, British Columbia Lumberm. 37(5):42, 90, 92; Ross and Jones, 1953, Canada Dept. Agric. For. Ins. Surv. Rept. 1952:133; Wright, 1953, Proc. West. For. Conserv. Assoc. 43:153; Anonymous, 1953, U. S. Dept. Agric. Portland For. Ins. Lab. Rept. 1952:30; Evans and Silver, 1954, Canada Dept. Agric. For. Ins. Surv. Rept. 1953:139; Glascock, 1954, Proc. West. For. Conserv. Assoc. 44:45; Hoyt, 1954, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1952-53:21; Knight and Wilford, 1954, U. S. Dept. Agric. Rocky Mtn. For. Range Expt. Sta. Ins. Cond. Rept. 1953:4; Orr, 1954, U. S. Dept. Agric. Intermtn. For. Range Expt. Sta. Ins. Cond. Rept. 1953:1; Ross, 1954, Canada Dept. Agric. For. Ins. Surv. Rept. 1953:142; Bailey, 1955, U. S. Dept. Agric. Intermtn. For. Range Expt. Sta. Rept. 1954:41; Cornelius, 1955, Jour. Forestry 53:711; Cornelius, 1955, Proc. West. For. Conserv. Assoc. 45:50; Cowlin, 1955, U. S. Dept. Agric. Pacific Northw. For. Range Expt. Sta. Rept. 1954:31, 37; Evenden and Wright, 1955, U. S. Dept. Agric. For. Serv. For. Pest Leaf. 5, 4 p.; Fang and Allen, 1955, Jour. Econ. Ent. 48:79; Kinghorn, 1955, Jour. Econ. Ent. 48:501, 503; Silver and Ross, 1955, Canada Dept. Agric. For. Ins. Surv. Rept. 1954:117; Spaur, 1955, Oregon St. Bd. For. Bien. Rept. St. For. 1952-54:42; Anonymous, 1955, California For. Pest Contr. Act. Comm. For. Ins. Cond. 1954:6, 8; Anonymous, 1955, U. S. Dept. Agric. For. Serv. Imp. For. Ins. 1954:2, 4, 7, 10; Anonymous, 1955, U. S. Dept. Agric. Pacific Northw. For. Range Expt. Sta. For. Ins. Surv. 1954:23; Anonymous, 1956, U. S. Dept. Agric. Pacific Northw. For. Range Expt. Sta. For. Ins. Surv. 1955:27, 40; Bailey, 1956, U. S. Dept. Agric. Intermtn. For. Range Expt. Sta. Rept. 1956:29, 32; Chapman and Wilson, 1956, Jour. Econ. Ent. 49:427; Cowlin, 1956, U. S. Dept. Agric. Pacific Northw. For. Range Expt. Sta. Rept. 1955:34, 37; Gardiner, 1956, Canada Min. Agric. Rept. 1954-55:17; Hagenstein and Furniss, 1956, Proc. Soc. Amer. For. 1955:167; LeJeune, 1956, British Columbia Dept. Lands For. For. Serv. Rept. 1955:80; McArdle, 1956, U. S. Dept. Agric. For. Serv. Rept. 1955:12;

Lu and Bollen, 1956, Proc. Soc. Amer. Bact. 56:35; Ostmark and Wilford, 1956, U. S. Dept. Agric. Rocky Mtn. For. Range Expt. Sta. Pap. 22:5, 13; Phipps, 1956, Oregon St. Bd. For. Bien. Rept. St. For. 1954-56:29; Price, 1956, U. S. Dept. Agric. Rocky Mtn. For. Range Expt. Sta. Rept. 1955:21; Rudinsky and Vité, 1956, For. Sci. 2:258; Silver and Ross, 1956, Canada Dept. Agric. For. Ins. Surv. Rept. 1955:93; Walters, 1956, Canada Dept. Agric. Pub. 975, 11 p.; Yasinski, 1956, U. S. Dept. Agric. Rocky Mtn. For. Range Expt. Sta. Pap. 23:1, 3; Cowlin, 1957, U. S. Dept. Agric. Pacific Northw. For. Range Expt. Sta. Rept. 1956:25; Gibson, 1957, Jour. Econ. Ent. 50:266; Kahn, 1957, Canadian Jour. Zool. 35:519; Lu, 1957, For. Sci. 3:336; Price, 1957, U. S. Dept. Agric. Rocky Mtn. For. Range Expt. Sta. Rept. 1956:81, 84, 86; Silver and Ross, 1957, Canada Dept. Agric. For. Ins. Surv. Rept. 1956:81, 86; Vité and Rudinsky, 1957, For. Sci. 3:156; Whiteside, 1957, U. S. Dept. Agric. Pacific Northw. For. Range Expt. Sta. For. Ins. Cond. 1956:2, 5, 31, 43; Atkins and Chapman, 1957, Canadian Ent. 89:80.

This species is very closely allied to *simplex*, but may be distinguished by the larger size, by the more strongly protubrant, more finely punctured, subgranulate, irregular surface of the frons (Fig. 23), by the more finely punctured pronotum, by the finer punctures of the declivital interspaces, and by the distribution (Fig. 62).

Male.—Length 4.4-7.0 mm. (average about 5.5), 2.3 times as long as wide; body color very dark brown, with reddish brown elytra.

Frons broadly convex, protruding rather strongly on lower half, inflated area arising abruptly just above smooth, elevated rim of epistomal margin; epistomal process about a fourth (0.24 times) as wide as distance between eyes, its arms very strongly oblique (about 80° from the horizontal) and usually not elevated, the horizontal portion about three-fourths its total width, flat, overlapping and apparently flush with or exceeding epistomal margin and bearing under its distal margin a dense brush of yellowish setae; surface irregular, rather finely, closely punctured and becoming granulate on lower half. Vestiture sparse, rather short, fine inconspicuous.

Pronotum 1.4 times as wide as long, widest at base; sides weakly arcuate and converging toward the strong constriction just behind the broadly, shallowly emarginate anterior margin; surface smooth and shining, the punctures rather small, irregular in size, close, deep; median line narrowly impunctate posteriorly (usually); vestiture moderately abundant, fine and rather short on disc, longer and coarse laterally.

Elytra 2.5 times as long as pronotum; sides straight and subparallel on basal two-thirds, rather broadly rounded behind; basal margins arcuate and bearing a row of about ten rather large, raised, overlapping crenulations, with several smaller submarginal ones particularly on interspaces two and three; striae weakly impressed, the punctures rather large and moderately deep, usually decreasing slightly in size toward base; interstriae about one and one-half times as wide as striae and armed by abundant, confused, transverse crenulations, each averaging almost half the width of an inter-

space, a few two-thirds as wide on posterior half of disc. Declivity rather steep, convex, with sutural interspace very strongly elevated and interspace two weakly impressed; striae rather deeply impressed, the punctures half as large as on disc; interstrial punctures rather fine, abundant and confused on one and three, almost uniseriate on two; none of the punctures granulate. Vestiture rather coarse, slightly longer on declivity, the longest setae equal in length to about one and one-half times the width of an interspace.

Female.—Very similar to male except declivital interspaces with smaller punctures and each with a median row of very coarse, somewhat pointed tubercles, the tubercles spaced by a distance slightly less than width of an interspace.

Type locality.—Grants Pass, Oregon. The type was studied.

Hosts.—*Pseudotsuga taxifolia*, *P. macrocarpa*, and less commonly from *Larix occidentalis* and *Tsuga heterophylla*.

Distribution.—Western United States, Alberta and British Columbia.

Specimens from the following localities were examined (Fig. 62). ARIZONA: Chiricahua Mts., Flagstaff, San Francisco Mts., and Santa Catalina Mts. CALIFORNIA: Alameda Co., Alma, Bean Ck., Big Basin, Boulder Ck., Callahan, Camp Meeker, Chester, Coulterville, Dead Horse Summit in Siskiyou Co., Fieldbrook, Foresthill, Gaberville, Green Point, Guerneville, Hackamore, Half Moon Bay, Happy Camp in Siskiyou Co., Honda, Laguinitas, La Honda, Lights Ck., McCloud, Meadow Valley, Moffat Ck. in Siskiyou Co., Mohawk, Palo Alto, Placerville, Point Reyes, Quincy, Santa Cruz, Trinity Co., Upper Lake in Lake Co., Wrights, and Yellow Ck. COLORADO: Colorado Springs, Ft. Garland, Gunnison N. F., Moffat, Pagosa Springs, Palmer Lake, San Isabel N. F., San Juan N. F., and Saguache. IDAHO: Beaver Canyon in Nez Perce Co., Beaver Ck. in Logan Canyon, Henry's Lake, Kooskia, Kootenai, Pioneerville, Priest River, Sandpoint, Smiths Ferry, and Stites. MONTANA: Apgar, Belton, Bozeman, Columbia Falls, Fish Ck. Station, Kalispell, Lake McDonald, Middle Ck. in Gallatin Co., and Ovando. NEW MEXICO: Capitan, Cloudcroft, Santa Fe, Tres Ritos, and Vermejo Pk. OREGON: Ashland, Clover Ck., Cold Springs, Corvallis, Detroit, Dixie Pass, Elk Ck., Forest Grove, Grants Pass, Hood River, Jewell, Klamath N. F., MacDonald Forest, Mary's Peak, Mistletoe, Mt. Angel, Myrtle Point, Newport, Oregon Caves, Otis, Philomath, Pinehurst, Portland, St. Helens, Salmon River, Santiam N. F., Siskiyou Mts., Sumpter, Tillamook, Tiller, and Waldo. UTAH: Cache N. F., Logan Canyon, Panguitch, Parowan Canyon, Provo Canyon, and Sanford Canyon. WASHINGTON: Ashford, Buckeye, Curlew, Des Moines, Easton, Fairfax, Grays Harbor City, Hoodsport, Hoquiam, Kent, Keyport, La Grande, Longmire, Meredith, Metaline Falls, Monroe, Mt. Rainier N. P., North Bend, Northport, Orting, Payallup, Port Angeles, Port Williams, Pullman, Quinalt, Sappho, Satsop, Seattle, Shelton, Stimson Ck. in Mason Co., and Vancouver. ALBERTA: Waterton. BRITISH COLUMBIA: Australian, Babine Lake, Barriere, Bestwick, Boston Bar, Britain River, Buttle Lake, Campbell River, Canim Lake, Cowichan Lake, Cumberland, Fernie, Fraser River Valley, Grant Lake, Hamilton Lake, Kamloops, Kettle River Valley, Lac LaHache, Lillooet River Valley, Lumby, Macalister, Merritt, Nimpkish Valley, Okanagan Lake, Prince George, Quesnel, Seymour Narrows, Soda Ck., Trinity Valley, Upper Campbell Lake, Vancouver, Vernon, West Kettle River Valley, Williams Lake, Windermere Lake, and Wogs Lake.

Geographical variation.—Not evident in the material at hand.

Biology.—This is a primary insect enemy of Douglas Fir. Although estimates of damage inflicted by it are not available for

all regions where it occurs, it probably is responsible for an average annual loss in excess of a half billion board feet of timber.

The winter is passed chiefly as young adults, although some larvae and parent adults also overwinter successfully. Flight activity may begin as early as the first of April and evidently continues at least until early September. Two principal periods of flight activity occur, the first during May or June is composed of overwintered young adults, the second during July or August is composed of beetles that overwintered as larvae and of parent adults re-emerging from their first set of galleries. The exact timing of each principal flight period may vary from locality to locality with altitude, latitude, exposure, peculiarities of a particular season, or other local ecological factors.

Ordinarily the material selected for attack includes stumps, windfalls, broken logs, or other injured or prostrate trees larger than eight inches in diameter. However, when populations are high or when assisted by draught, healthy, vigorous standing timber may be selected. The attack on a standing tree usually begins in the upper midbole area and progresses upward and downward from that point. In prostrate material, at least when the bark is relatively thick, the beetles attack the sides and upper surfaces as well as the lower. The attack is slow and continuous, without any sudden or concerted swarming of the beetles. Its duration is variable, evidently depending on the population density of beetles in the area, upon resistance of the host, or upon local climatic or other local ecological factors. It may be completed in a few days or it may continue for more than a year and involve two or possibly more successive generations.

The egg galleries (Fig. 63) are constructed almost entirely in the inner bark; they are in continual contact with the cambium and may very lightly score or at least stain the wood. They are straight or nearly so, and parallel the grain of the wood.

The initial attack is made by the female beetle in a crevice of the bark. Soon after beginning the attack she is joined by a male who takes over the function of removing frass from the entrance hole. Mating evidently occurs within a few hours after the cambium is reached. After the gallery has been extended several centimeters the male may pack the lower areas with frass thereby closing the entrance hole, or he may leave the gallery in search of another female. Most of the galleries are from about 12 to 30 cm. in length, but are known to exceed 90 cm. As with other species, ventilation tunnels are placed at irregular intervals, or they may be entirely absent. The maximum number of ventilation tunnels counted in more than a hundred galleries measured during this study was four; about 80 percent of the galleries had two ventilation tunnels.

Oviposition may begin within two or three days after the attack; according to Vité and Rudinsky (1957:157) the first eggs, under controlled laboratory conditions, may appear within 36 hours after the attack begins. Eggs evidently may be found throughout the

Fig. 63. *Dendroctonus pseudotsugae*: Egg galleries longitudinal, straight; eggs deposited in grooves, each oriented with its long axis perpendicular to egg gallery; larval mines usually independent, almost never cross, but may join one another during final stages of development.

period of summer activity until about early September. According to Chamberlin (1918:20) one female may produce as many as 160 eggs in one gallery; the maximum number counted during this study was 102 in a gallery only partly complete.

Eggs are deposited in grooves about two to four millimeters deep along the sides of the gallery, near but not necessarily touching the cambium. The grooves are placed alternately on the sides, without overlapping or without more than a few millimeters between the end of the groove on one side and the beginning of the next on the other side. The grooves vary considerably in length, they range from less than one to more than eight centimeters. The eggs are deposited

in a single row in contact with one another and oriented with the long axis perpendicular to the egg gallery and more or less parallel to the cambium. It is presumed that the larvae emerge from the egg at the end farthest from the egg gallery. This habit of orienting the eggs is peculiar in the genus among the species observed personally during this study, and presumably is associated with the fact that the larvae construct independent mines, rather than working in congress as with other species that deposit masses of eggs in common grooves. The eggs are held in position by a rather thick layer or partition of coarse, fibrous frass that separates them from the egg gallery. Following the period of oviposition most of the females re-emerge to construct a second set of galleries.

The period of incubation varies considerably with various factors, particularly temperature. Vité and Rudinsky (1957:161) found, under controlled conditions, that it ranged from about 6 to 28 days. Under field conditions estimates of the incubation period range from 8 to 24 days. Under controlled conditions, Vité and Rudinsky (1957:161) found that larval development required about 19 to 72 days and the pupal period about 5 to 18 days. The larvae construct individual mines more or less perpendicular to the egg gallery and are in continual contact with the cambium area. They increase gradually in diameter and tend to fan out somewhat as they progress. Unless crowding occurs they normally do not cross one another. Near the end of larval development a pupal chamber may be cleared in the cambium area at the end of the larval mine, or the larva may bore out into the bark for a variable distance before pupating. The young adults overwinter in the brood galleries and emerge the following spring. Larvae that develop from eggs deposited in the fall may not mature before the onset of cold weather and, therefore, pass the winter as larvae. These larvae mature early in the following summer and may emerge in July or August, or, evidently, they may overwinter in the brood galleries (Bedard, 1950:9). There is one complete generation and possibly a partial second generation each year.

Material Examined

Although an exact count was not kept during this study, it is estimated that the number of specimens examined exceeded the following figures: *brevicomis*, 2000; *frontalis*, 400; *parallelocollis*, 500; *adjunctus*, 500; *ponderosae*, 2000; *aztecus*, 26; *terebrans*, 200; *valens*, 2000; *micans*, 150; *punctatus*, 200; *murrayanae*, 400; *obesus*, 5000; *simplex*, 300; *and pseudotsugae*, 2000. The distribution maps and records treated in the discussion of each species indicate where these species were collected.

The holotypes of species studied include: *brevicomis* Leconte, *barberi* Hopkins, *frontalis* Zimmerman, *arizonicus* Hopkins, *mexicanus* Hopkins, *approximatus* Dietz, *convexifrons* Hopkins, *ponderosae* Hopkins, *monticolae* Hopkins, *jeffreyi* Hopkins, *aztecus*

Wood, *valens* Leconte, *beckeri* Thatcher, *punctatus* Leconte, *johanseni* Swaine, *murrayanae* Hopkins, (*Hylurgus*) *obesus* Mannerheim, *piceaperda* Hopkins, *engelmanni* Hopkins, *borealis* Hopkins, *similis* Leconte, *simplex* Leconte, and *pseudotsugae* Hopkins. In addition, the types of *adjunctus* Blandford and of *rufipennis* Kirby were compared to my specimens by Dr. R. T. Thompson at the British Museum of Natural History. The types of *parallelocollis* Chapuis, *terebrans* Olivier, and of *micans* Kugelann were not examined; specimens of *parallelocollis* that were compared to the type for Hopkins were studied, however. Because *micans* is the only European species in the genus there was no problem with its identity.

Biological studies of the various species were conducted by myself in the following localities: *brevicomis* at Flagstaff, Prescott and Williams, Arizona, Dixie N. F., Salina and Ashley N. F., Utah, Plumas N. F. and Lassen N. F., California, and near Sisters, Oregon; *frontalis* at Prescott, Arizona; *parallelocollis* at Dixie N. F., Salina and Sanford Canyon, Utah, Prescott and Williams, Arizona, and Texmelucan, Puebla (Mexico); *adjunctus*, Dixie N. F., Sanford Canyon, and Panguitch, Utah, and Prescott, Arizona; *ponderosae*, Logan Canyon, Ashley N. F., Wasatch N. F., Salina, Panguitch, Sanford Canyon, La Sal Mts., and Dixie N. F., Utah, Flagstaff, Arizona, Fallen Leaf Lake, Lassen N. F., and Tahoe N. F., California, and Ochoco N. F., Oregon; *aztecus*, Coapala, Sinaloa (Mexico); *terebrans*, Kingsland, Georgia; *valens*, Logan Canyon, Ashley N. F., and Panguitch Lake, Utah, Lassen N. F., and Yreka, California; *murrayanae*, Logan Canyon, and Wasatch N. F., Utah; *obesus*, Santa Fe Ski Basin, New Mexico, Logan Canyon, Wasatch N. F., Ashley N. F., Dixie N.F., Utah, Gold Lake and Cascade Head Expt. For., Oregon; and *pseudotsugae*, Logan Canyon, and Sanford Canyon, Utah, Siskiyou Co., California, and Mary's Peak, Oregon.

The hosts and localities included in this study are restricted to those recorded for specimens examined during the study. When localities were not known to me and could not be located on available maps, the locality designation was placed in quotation marks. The scientific name of Douglas fir used here is *Pseudotsuga taxifolia*, as employed by R. J. Preston (1961, North American Trees, p. 63), not *P. menziesii* as currently employed in the checklist.

References to the vast quantity of literature treating *Dendroctonus* species is listed in the synonymies and is thought to be fairly complete to 1958 for all species except *micans*. About two-thirds to three-fourths of the articles listed were examined; mechanical problems made it impossible to examine all sources or to locate and review all recent articles. The disadvantages in this approach are obvious; undoubtedly some injustices and errors have resulted. Because no real taxonomic problem involved the European *micans*, an extensive effort to locate references to this species was not made. In treating the biologies of all species it was arbitrarily decided that when three principal authors who included original data in their reports agreed on a particular point, that point was considered as

common knowledge, if it more or less agreed with my observations, and literature citations were not included. In a few instances where contradictory data were presented, all pertinent articles were studied and a decision was made as to the accuracy of the report.

Acknowledgement

The contributions and cooperation of numerous individuals and organizations have made possible the completion of this study. The writer is indebted to M. L. Prebble, Forest Entomology and Pathology Branch, Canada Department of Forestry, for providing in 1955 the initial stimulus and encouragement to undertake a revision of this difficult and important genus of forest insects. Appreciation is also expressed to the U. S. National Museum, to the Museum of Comparative Zoology, to the Museum Zoologicum Univesitatis (Helsinki), to the Canadian National Collection of Insects, to the Portland (Oregon), Berkeley (California), and Albuquerque (New Mexico) regional laboratories of the Forest Service, U. S. Department of Agriculture, to the University of California (Berkeley) and to the Oregon State University for making available facilities and/or specimens for this study. Special thanks are also due to J. B. Thomas (Sault Ste. Marie), George R. Hopping (Calgary), and D. A. Ross (Vernon), Forest Entomology and Pathology Laboratories, Canada Department of Forestry, for special notes and specimens; to R. W. Stark and David L. Wood, Department of Entomology and Parasitology, University of California (Berkeley), and to R. L. Furniss, Forest Service, U. S. Department of Agriculture, for council and direction in arranging field studies and especially for their kindness in reviewing the manuscript of this paper. Of the many forest rangers and entomologists contacted for direction and advice in locating local infestations, special mention should be made for the kindness and special assistance of Vern P. Yerkes, Cascade Head Experimental Forest (Otis, Oregon). Sincere thanks are also expressed to Donald E. Bright, Jr., to Jay B. Karren, and to Howard P. Shurtleff for the many weeks they spent gathering biological data throughout the western United States from 1960 to 1962, for this project. Appreciation is also expressed to the National Science Foundation for the financial aid necessary to conduct the field work that was so vital to this study.

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A SURVEY OF THE HERPETOFAUNA OF THE DEATH VALLEY AREA

Frederick B. Turner and Roland H. Wauer[1]

Since the report of the Death Valley Expedition of 1891 (Stejneger, 1893), there have been only incidental notes on the herpetofauna of the Death Valley area of eastern California. Specimens were collected by Grinnell and Dixon in 1917 and 1920; and Joseph Slevin of the California Academy of Sciences collected in the Panamint Mountains in the early 1930's. At about the same time, Klauber prepared a tentative list of amphibians and reptiles known from the area (unpublished). Death Valley National Monument was established in 1933 and during 1939 and 1940, Park Naturalist Wilbur Doudan collected specimens for the National Park collection. During the late 1940's Stebbins made several collecting trips to the area. During the winters of 1953-54 and 1954-55, Frederick B. Turner collected for the National Park Service, and Roland H. Wauer collected specimens during his five years residency from 1957 through 1962.

The writers have drawn on field notes of Joseph Grinnell, Joseph Dixon, Robert C. Stebbins, Richard G. Zweifel, Robert Glaser and data available in the files of the Death Valley National Monument. We wish to thank Matt Ryan, Ralph and Florence Welles, Warren Hill and Dick Davis for additional data. Records are included from the American Museum of Natural History, the University of California Museum of Vertebrate Zoology and the California Academy of Sciences.

The Area

The arid valleys and mountain ranges of Inyo County, California, are physiographically a part of the Great Basin Desert. However, the Death Valley area is characterized by higher temperatures and less rainfall than most of the Great Basin, so there is a strong affinity with the Mojave Desert. The area is roughly that of Death Valley National Monument, which includes small sections

1. Laboratory of Nuclear Medicine and Radiation Biology, University of California, Los Angeles; and U. S. National Park Service, Zion National Park, Utah.

of Nye and Esmeralda Counties, Nevada; and San Bernardino County, California. The Panamint Range forms the western edge of Death Valley and rises to a height of 11,049 feet at the summit of Telescope Peak. The Panamint crest is nowhere below 4500 feet and four distinct zonal formations exist. The Amargosa Range forms the eastern edge of Death Valley and exists wholly within the Lower Sonoran Life Zone, except for an area in the Grapevine Mountains where a pinon-juniper association is present between 5500 and 6700 feet elevation. The valley itself is an elongated fault basin, of which 550 square miles lie below sea-level. It extends for 140 miles from Ubehebe Crater, south to Saratoga Springs. The lowest point is near Badwater, - 282 feet.

Habitats

From the floor of Death Valley Telescope Peak rises over 11,330 feet from the salt pan of Death Valley. The huge dry lake bed is "a chemical desert not fit to sustain life" (Wauer, 1962). Surrounding the salt pan is a line of phreatophytes (deeply rooted plants) which separates the salt flats from the gravels of the alluvial fans. Only where the fans dip very steeply into the playa itself is there a distinct demarcation between the salt and gravels. Iodine bush (*Allenrolfea occidentalis*)grows in isolated bunches nearest the salts, and saltgrass (*Distichlis stricta*) and arrowweed (*Pluchea sericea*) occur next. The dominant species of this zone is honey mesquite (*Prosopis juliflora*). Mesquite occurs in large stands at Coyote Well, north and south of Bennett Well, on the Furnace Creek fan, south of Salt Creek, and in Mesquite Valley. Sacatone grass (*Sporobolus airoides*) and desert holly (*Atriplex hymenelytra*) occur next and mingle with creosote bush (*Larrea divaricata*).

Fresh water occurs at only a few places on the valley floor. Potable water flows from Mesquite Springs along an irrigation ditch for almost a quarter-mile. Furnace Creek Ranch offers many irrigation ditches and open ponds and a wide range of exotic plants such as tamarisk (*Tamarix*) and date palms (*Phoenix*). Tule Spring and Eagle Borax Works are along the western edge of Death Valley amid the line of phreatophytes. A pool of stagnant water persists at Tule Spring and perennial pools of water exist at Eagle Borax Works. Perennial pools also exist at Coyote Well and along the Amargosa riverbed which flows north down the center of Death Valley. Saratoga Springs is a large oasis in the southern end of the valley where a two-acre lake occurs.

In the north-central portion of the valley there are twenty-five square miles of sand dunes. Mesquite and saltgrass occur in isolated stands throughout the dunes. Arrowweed grows along the southern end of the sands and continues south to a brackish stream called Salt Creek. This flow reaches the center of the valley in late spring and is completely dry during the summer. Sand dunes also exist just south of Saratoga Springs.

The alluvial fans extend from the salt pans as much as twelve miles, or as little as twenty or thirty feet, before reaching the mouths of canyons. In the Amargosa Range the canyons and washes begin almost immediately above the salt pan. The gravels of the larger fans, such as those from Cottonwood, Emigrant, Monarch, Blackwater, Titus, Furnace Creek, Hanaupah and Johnson Canyons, cover many hundreds of square miles. Creosote bush is dominant here, but desert holly, fourwinged saltbrush (*Atriplex canescens*), bursage (*Franseria dumosa*), honey sweet (*Tidestromia oblongifolia*), and brittlebush (*Encelia farinosa*) are usually present.

The rocky canyons support a more diverse plant growth than the previously mentioned areas. Here, again, is creosote bush, greenmolly (*Kochia americana*), cliffrose (*Cowania mexicana*), globemallow (*Sphaeralcea eremicola*), rabbitbrush (*Chrysothamnus*), and desert fir (*Peucephyllum schotti*). Vegetation also grows along the canyon walls, such as stingbush (*Eucnide urens*) and Death Valley sage (*Salvia funerea*). Because of the restricted flow of occasional large amounts of water, the canyons tend to be well scoured and support few large shrubs except along the edges. The main channels, or washes, are a jumble of rocky debris.

A line of springs occur through the Panamint Range between 3500 and 4500 feet elevation. Heavy growths of willow (*Salix*), rabbitbrush and *Baccharis*, and in a few places cottonwood (*Populus fremonti*), are the dominants. Desert grape (*Vitis girdiana*) grows in abundance in Hanaupah and Cottonwood Canyons.

Large open sage flats occur directly below the pinon-juniper woodlands. Examples of this habitat are Greenwater, Amargosa, and Butte Valleys; and Old Crump, Wildrose, Rabbit ,and Harrisburg Flats. Vegetation consists primarily of shadscale (*Atriplex confertifolia*), cliffrose, blackbrush (*Coleogyne ramosissima*), bladdersage (*Salazaria mexicana*), big sagebrush (*Artemisia tridentata*) and cottonthorn (*Tetradymia spinosa*).

The pinon-juniper woodlands of the Panamint and Grapevine Mountains occur between about 5500 feet and 8000 feet elevation. Juniper (*Juniperus osteosperma*) and pinon (*Pinus monophylla*) dominate the zone. Less dominant forms are desert sage (*Salvia carnosa*), big sagebrush and cottonthorn. At the upper limits of the pinon-juniper zone is mountain mahogany (*Cercocarpus ledifolius*). The woodlands, constituting the Upper Sonoran Life Zone, give way to a transition zone dominated by limber pine (*Pinus flexilis*), water birch (*Betula frontalis*), currant (*Ribes cereum*) and service berry (*Amelanchier alnifolia*). Above 10,000 feet, in the Boreal Zone, bristlecone pine (*P. aristata*) is dominant.

The Herptofauna

Three species of amphibians and thirty-five species of reptiles have been reported on good evidence.

The Valley Floor: The desert oases support small populations of amphibians and reptiles. Red-spotted toads (*Bufo punctatus*) are

List of Species and Races	Valley Floor	Alluvial Fans	Canyons, Washes	Canyon Springs	Sage Flat	Pinon-Juniper	Trans., Boreal
Amphibians							
Bufo punctatus	X			X			
Hyla regilla	X			X			
Rana catesbeiana	X						
Reptiles							
Gopherus agassizi		X	X				
Coleonyx v. variegatus	X	X	X				
Dipsosaurus d. dorsalis	X	X	X				
Crotaphytus collaris baileyi		X	X				
Crotaphytus w. wislizeni	X	X	X				
Sauromalus o. obesus		X	X		X		
Callisaurus draconoides gabbi	X	X	X		X		
Uma notata scoparia	X						
Sceloporus magister			X		X	X	
Sceloporus occidentalis biseriatus			X	X	X	X	
Sceloporus graciosus gracilis						X	X
Uta stansburiana stejnegeri	X	X	X	X	X	X	
Uta graciosa	X						
Phrynosoma platyrhinos calidiarum		X	X		X		
Gerrhonotus panamintinus			X	X			
Xantusia vigilis			X		X	X	
Cnemidophorus t. tigris	X	X	X	X	X		
Eumeces gilberti							
Leptotyphlops h. humilis			X	X	X		
rubricaudatus	X		X				
Lichanura roseofusca gracia			X				
Masticophis flagellus piceus	X	X	X	X	X		
Masticophis t. taeniatus			X			X	
Salvadora h. hexalepis		X	X		X		
Phyllorhynchus decurtatus perkinsi		X	X				
Arizona elegans			X				
Pituophis catenifer deserticola		X	X		X	X	
Lampropeltis getulus californiae			X		X		
Rhinocheilus lecontei clarus			X		X		
Sonora semiannulata isozona		X	X		X		
Sonora semiannulata linearis			X				
Chionactis o. occipitalis			X		X		
Trimorphodon vandenburghi			X				
Hypsiglena torquata deserticola			X	X	X		
Tantilla utahensis			X				
Crotalus mitchelli stephensi		X	X	X	X	X	
Crotalus c. cerastes	X	X	X				

Table 1. Distribution of the amphibians and reptiles of the Death Valley area, Inyo County, California.

found at Saratoga Springs, Eagle Borax Works, Furnace Creek Ranch and Inn, and Cow Creek. There are isolated groups in Furnace Creek Wash and in all of the Texas Spring drainages (Turner, 1959a). Toads also occur around the canyon springs in the Lower Sonoran Life Zone. Records exist from Johnson, Hanaupah, Emigrant and Cottonwood Springs. The Pacific tree frog (*Hyla regilla*) has a similar range, but is found in the valley at Saratoga Springs and near Scotty's Castle only. The bullfrog (*Rana catesbeiana*) exists at Furnace Creek Ranch and Inn where it was introduced about 1920.

The most common reptile of the valley oases is the side-blotched lizard (*Uta stansburiana*). It is present throughout the year except during the coldest days, and has been found several feet onto the salt pan, probably in search of insects and spiders that occur in this unproductive area. *Uta* have been found throughout the Lower Sonoran Life Zone. The banded gecko (*Coleonyx variegatus*) occurs about the desert oases also, but is nocturnal. One was collected at 4000 feet in Wildrose Canyon.

The worm snake (*Leptotyphlops humilis*) has been found from below sea-level to about 4000 feet. The most common snake of the valley oases is the desert whipsnake (*Masticophis flagellum*). It occurs about the mesquite and tamarisk growths at Furnace Creek Ranch, Eagle Borax Works, Mesquite Spring and Stove Pipe Wells Hotel, and frequents the washes and canyons and the open sage flats below the pinon-juniper association. The only other reptile occasionally found at the valley oases is the sidewinder (*Crotalus cerastes*), which prefers the low alluvial fans and washes but rarely is found at the oases such as Furnace Creek Ranch and Eagle Borax Works. Records exist throughout the lower half of the Lower Sonoran Life Zone.

The sand dunes of Death Valley afford another habitat. The fringe-toed lizard (*Uma notata*) and long-tailed uta (*Uta graciosa*) have been found in the dunes south of Saratoga Springs (Norris, 1958). The dunes located in the central portion of Death Valley are inhabited by banded geckos, gridiron-tailed lizards (*Callisaurus draconoides*), side-blotched lizards and sidewinders.

Wherever mesquite is prevalent there occurs an additional group of reptiles. Here is the crested lizard (*Dipsosaurus dorsalis*), which ranges up into the low canyons and washes where mesquite exists. The whiptail lizard (*Cnemidophorus tigris*) also occurs in mesquite thickets, and is present in the low canyons and washes in the Lower Sonoran Life Zone. Other species found in the mesquite thickets are the banded gecko, the side-blotched lizard, the desert whipsnake and the sidewinder.

The Alluvial Fans: Of the reptiles discussed so far, all but *Uma* and *Uta* occupy alluvial fans above the valley floor. Other species exist where the gravel and creosote bush habitat persists. The desert tortoise (*Gopherus agassizi*) has been found from 1500

to 3500 feet elevation and is never common. It is sometimes found on the open fans and washes and even on the sage flats. Both collared lizards (*Crotaphytus collaris*) and chuckwallas (*Sauromalus obesus*) occur where the fans are sprinkled with large boulders. The chuckwalla often is found below sea-level where the fans meet the salt pans (e.g., below Sheep, Willow Creek and Johnson Canyons). There are no records from the Upper Sonoran Life Zone.

The carnivorous leopard lizard (*Crotaphytus wislizeni*) occurs from below sea-level into the canyons and washes, and even into the pinon-juniper woodland. The horned lizard (*Phrynosoma platyrhinos*) is rarely found at lower elevations, but prefers the upper slopes amid creosote bush. In similar areas the patch-nosed snake (*Salvadora hexalepis*), the leaf-nosed snake (*Phyllorhynchus decurtatus*), the gopher snake (*Pituophis catenifer*), the ground snake, *Sonora semiannulata*), Mitchell's rattlesnake (*Crotalus mitchelli*) and the sidewinder occur. Patch-nosed snakes are not common, but a few records exist from the upper alluvial fans and canyons to about 4500 feet. The gopher snake frequents the same zones, but is more common and often occurs around canyon springs. Mitchell's rattlesnake frequents alluvial fans but rarely is found below sea-level. It has been collected at Mahogany Flat (8200 ft.) so it can be expected throughout the Lower and Upper Sonoran Life Zones.

The Canyons and Washes: Most of the species already discussed range into canyons and washes. In fact, twenty-seven species of reptiles have been reported here. Twelve species, not so far mentioned, are found in this habitat. The spiny lizard (*Sceloporus magister*) has been found in the upper canyons of the Lower Sonoran Life Zone such as Cottonwood and Emigrant Canyons; and also on the higher flats below the pinon-juniper woodland and in the forest itself. Records exist from 3900 to 7000 feet elevation. The range of the western fence lizard (*Sceloporus occidentalis*) is very similar. The alligator lizard (*Gerrhonotus panamintinus*) was first reported by Stebbins (1958)in Surprise Canyon. The night lizard (*Xantusia vigilis*) has been collected in Monarch Canyon, near Dante's View, and among pinon pines to 9360 feet in the Panamint Mountains (Turner, 1959c).

The desert boa (*Lichanura roseofusca*) has been found in Hanaupah and Emigrant Canyons (Turner, 1959b). A striped whipsnake (*Masticophis taeniatus*) was taken at Willow Creek (5400 feet) in 1891, and another found near Hunter Spring in the pinon forest. The California king snake(*Lampropeltis getulus*) prefers open canyons above 3900 feet. Records exist from Johnson and Wildrose Canyons; and for the sage flats such as Wildrose and Harrisburg Flats. Other species found in this habitat are the long-nosed snake (*Rhinocheilus lecontei*), the shovel- nosed snake (*Chionactis occipitalis*), the lyre snake (*Trimorphodon vandenburghi*), the night snake (*Hypsiglena torquata*), and the black-headed snake (*Tantilla utahensis*). The latter has been found in Surprise Canyon only.

The Canyon Springs: The red-spotted toad and the Pacific tree frog have been found here, as well as the western fence lizard, the desert whipsnake, the night snake, and Mitchell's rattlesnake. Gilbert's skink (*Eumeces gilberti*) is common among the grapevines in Hanaupah and Johnson Canyons (Rodgers and Fitch, 1947) and has also been recorded on Harrisburg Flat.

The Sage Flats: Most of the individuals found in the canyons and washes also occur in this vegetation type.

The Pinon-Juniper Woodlands: The species occurring in this habitat have already been discussed.

The Transition and Boreal Life Zones: The sagebrush lizard and the night lizard are the only two species known to occur above the pinon-juniper woodlands. The sagebrush lizard has been found above 10,000 feet, and *Xantusia* has been collected at 9360 feet in the Panamint Mountains.

List of Selected Records

The following is a selected list of reptiles that have not been previously reported from the Death Valley area, or that have been recorded on few occasions.

1. Western Worm Snake. *Leptotyphlops h. humilis*. This species was first reported by Klauber (1931) from Bennett Well, but since then additional individuals have been reported from below sea-level to 4000 feet at Wildrose. In April of 1960, during the reconstruction of Bennett, Shorty's and Gravel Wells, much of the planking was removed and replaced. Several blind snakes were found at each site, but a large aggregation of several dozen snakes was uncovered at Shorty's Well. They were situated beneath the board planking some four feet below the surface of the ground. A few individuals were collected and identified by Wauer.

2. Desert Leaf-nosed Snake. *Phyllorhynchus decurtatus perkinsi*. This species was first collected by Slevin near Mesquite Spring in April of 1935. It has since been found in Emigrant and Goler Canyons and recently Wauer collected a specimen at the edge of the salt pan (-150 feet) in May of 1961. The temperature at 8:30 p.m. was 85° F.

3. California King Snake. *Lampropeltis getulus californiæ*. This species has been found to be fairly common throughout the Panamint Range, but there are no localities from the Amargosa Range, east of Death Valley. Specimens were taken at Towne Pass, Wildrose and Johnson Canyons, and on Harrisburg Flat.

4. Desert Long-nosed Snake. *Rhinocheilus lecontei clarus*. The first specimen from the area was taken by Robert Glaser on Towne Pass, April 11, 1954. Wauer collected a specimen on Harrisburg Flat on June 23, 1962. The temperature at 3500 feet was 75° F.

5. Ground Snake. *Sonora semiannulata*. Two races have been recorded. The more abundant is *S. s. isozona*, the most common noc-

turnal snake in the area. Specimens have been taken from 2500 to 5200 feet elevation, in both the Panamint and Amargosa Ranges. *S. s. linearis* was collected in Wildrose Canyon on July 5, 1954, and identified by Klauber.

6. Mojave Shovel-nosed Snake. *Chionactis o. occipitalis.* This species was first collected by Arnold Applegarth in Furnace Creek Wash in March of 1954. Additional species have been taken in Goler Canyon, at Ballarat and at Ryan. The race intergrades with *talpina* along its northern limits which is the area immediately east of the Amargosa Range.

7. California Lyre Snake. *Trimorphodon vandenburghi.* A single specimen was collected by Wauer on Daylight Pass at 10 p.m. on June 26, 1962. It was taken at 4300 feet in a creosote bush habitat. The temperature was 78° F. On July 1, 1962, Warren Hill found a road kill in Furnace Creek Wash at 1500 feet elevation. The two locations are about 15 miles apart in the Amargosa Range. Both specimens represent easternmost records for the species. The Daylight Pass specimen was taken only ½ mile from the Nevada line. Both Schmidt (1953) and Stebbins (1954) show the range for this species as extending east from the California coast to the Argus Mountains. These records, then, increase the known range of this species by about 100 miles to the east.

Discussion

In general, the reptilian fauna of the Death Valley area includes a few widely distributed forms. (e.g., *Callisaurus*, *Uta*, *Cnemidophorus tigris*, *Masticophis flagellum*, and *Crotalus cerastes*), which present a fairly continuous distribution at lower elevations, except for the alkaline desert. However, many species exhibit disjunct patterns of distribution, the spottiness inversely proportional to the adaptive versatility of the species involved. Some of these latter forms are isolated on islands of suitable habitat afforded by the mountain ranges on each side of the valley (Miller, 1940; Stebbins, 1958). There is little known about the distribution of such forms. The Amargosa Range has had only slight study. The Panamint Range has been more intensively worked. The faunistic diversity of the Panamints, as opposed to the Amargosa Range, is due to this factor and to the fact that the latter is more uniform ecologically. In spite of numerous explorations of the Panamints, Stebbins (1958) has recently described a new *Gerrhonotus* from Surprise Canyon. Further work is apt to be comparably rewarding.

In view of the relatively high degree of endemism exhibited by Death Valley's plants, one might expect comparable differentiation among the fauna. The Death Valley area is the type locality for several insects and a half-dozen vertebrates. A concentration of type localities may or may not be indicative of conditions favoring the establishment of races and/or species. Here it probably is. In the case of populations occupying isolated montane areas, where the

duration of isolation may be inferred fairly accurately (i.e., from the Pleistocene recession of surrounding bodies of water), a comparison of such isolates may throw light on the rate at which morphological differences may become established. It is, of course, important to know that presumably disjunct populations are indeed genetically isolated.

We may also look ahead to future modifications of the desert areas of southeastern California, which will be subjected to continued exploitation in coming years. The encroachments are already of dismaying extent. While Death Valley National Monument is set aside as a preserve, the area has had large in-holdings and provisions for multiple use by individuals and mining concerns. Extensive records compiled now may be useful in evaluating the impact of heavier visitor use, or of construction and mining activity. Even since 1920, we may infer from Grinnell's notes that the area around Furnace Creek Ranch has been markedly changed. Although there has been no intention of maintaining this area under natural conditions, it serves as an example of how the original reptilian fauna has been impoverished. Grinnell recorded *Crotaphytus collaris*, *Phrynosoma*, *Dipsosaurus*, *Cnemidophorus*, *Callisaurus* and *Uta*, but only *Uta* remains in large numbers.

While the geographic limits of reptilian distributions are imposed by broad climatic regimes, the most difficult problems involve an explanation of the discontinuities within such overall ranges. The occurrence of some species is clearly linked with some attribute of the physical environment. An excellent example is afforded by the species of the genus *Uma*, which has been nicely treated by Norris (1958). Here one limiting factor is an appropriate substrate within the broad climatic limits suitable for the species. Certain otherwise suitable sand deposits are not occupied because of a lack of pathways for dispersal. Usually such problems are not so easily resolved. Klauber (1939) discussed data on the activity and distribution of snakes accumulated after some 100,000 miles of driving in southeastern California, commenting on time of day and year, temperature, moonlight, irrigation and habitat as factors influencing activity and distribution of snakes. Even after this, Klauber could not draw unequivocal conclusions as to the causal relations between the distribution of snakes and their environment.

Sometimes the distribution of a reptile coincides closely with that of a plant species, which is considered as an "indicator" for a particular widespread climatic regime. Yet the concordance is never perfect. There are places where the "indicator" occurs and not the reptile; and vice versa. For example, Stebbins (1948) has discussed the distribution of *Xantusia vigilis* and various species of *Yucca*. These cases, at best, merely tell us that the tolerance range of the animal is roughly comparable to that of the plant, and there is no indication of what limiting factors may operate within the range of the reptile, or upon what stage of the life cycle the limitation is imposed. Around Death Valley, chuckwallas occur only

in areas with large rocks or where there are sizable crevices in the walls of rocky canyons. The influence of vegetation, either as a direct source of food for herbivorous lizards, or as food for arthropods which are in turn eaten by carnivorous forms, has not been investigated. Nor do we know how interspecific competition for suitable shelter and basking sites, or possibly food, may influence distribution.

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THE SYSTEMATICS OF *CROTAPHYTUS WISLIZENI*, THE LEOPARD LIZARDS

PART I

A REDESCRIPTION OF *CROTAPHYTUS WISLIZENI WISLIZENI* Baird and Girard, AND A DESCRIPTION OF A NEW SUBSPECIES FROM THE UPPER COLORADO RIVER BASIN[1]

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One group of North American iguanid lizards to receive slight consideration for systematic studies has been the leopard lizard, *Crotaphytus wislizeni*. This species has a wide distribution occurring in most of the arid and semi-arid basins of western North America, *i.e.*, Great Basin, Upper Colorado River Basin [Painted Desert], Mojave Desert, San Joaquin Valley of central California, Colorado Desert, Sonora Desert, Chihuahua Desert, peninsular, and to a limited extent, insular Baja California. Throughout this extensive area, populations of *C. wislizeni* occur on the brushy low lands of the valleys, low foothills, and alluvial fans, seldom being found at elevations exceeding 6000 feet above sea level. In contrast to *Crotaphytus collaris*, the collared lizard, *C. wislizeni* is not restricted to rocky rough areas, but occurs where the soils are sandy or of loose gravel. Perhaps the densest populations are found in areas where rodent burrows have provided numerous holes for escape as well as underground tunnels used for shelter (aestivation and hibernation) and perhaps nesting.

We have been amazed that such a large, attractive lizard should escape the attention of systematic herpetologists for so long a time. Since April 1852, when Baird and Girard published the original description, not a single major study has been published on this species. Stejneger (1893) discussed the question of *wislizeni* and *silus*, but was apparently limited by insufficient material. Cope (1900), with the same material available as Stejneger, concluded by placing *silus* as a subspecies of *wislizeni*. Van Denburgh (1922), with additional material from the San Joaquin Valley, was able to describe the juvenile color pattern of *silus*, but did not attack the major problem associated with the variable adult patterns of other populations. Smith (1946) recognized the need to determine if *silus* is a valid species or a subspecies of *wislizeni*. His retention of *silus* as a subpecies of *wislizeni*, following the check list of Stejneger and Barbour (1943), left the problem essentially as it had been for many years.

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This study originated out of an extension of recent efforts which included this species in the Great Basin (Banta, 1963) and the Upper Colorado River Basin (Tanner. 1963). During our independent studies, opportunities were afforded each of us to make comparisons of the *wislizeni* populations from the Great Basin and adjacent areas to the south and east. Resulting from these studies were the independent realizations of the existence of a distinct population of leopard lizards in the Upper Colorado River Basin of eastern Utah and the adjacent states to the east and south, as well as the need to re-define *Crotaphytus wislizeni wislizeni.*

Crotaphytus wislizeni was originally described by Baird and Girard in April 1852 with the type locality listed as "near Santa Fè, New Mexico." Since then the following names have been proposed: *C. gambeli* Baird and Girard, 1852, type locality, "California"; *C. fasciatus* Hallowell, 1852, type locality, "Jornada del Muerte, New Mexico"[2]; *C. copeii* Yarrow, 1882, type locality, La Paz, Baja California Sur, Mexico; *C. silus* Stejneger, 1890, type locality, Fresno. California; *C. fasciatus* Mocquard, 1899, type locality, La Palmas, Baja California, Mexico.

Included in the synonomy of *Crotaphytus wislizeni* of Cope (1900:225) is "*Leisosaurus hallowellii* Aug. Duméril, vol. 8, 1856, p. 533, note 1." We are unable to determine the reason for this inclusion by Cope. We have checked the Duméril report and find that the name *Leiosaurus hallowelli* was proposed as another name for *L. fasciatus*, and although there were discussions of the similarities and differences between *Leiosaurus* and *Crotaphytus*, nowhere did he synonymize *Crotaphytus* with *Leiosaurus.* Guibé (1954:50) also lists *Leiosaurus fasciatus* Dumeril and Bibron, 1837, Erpet. Gen.. IV, p. 244, but does not mention *L. hallowelli.*

Baird (1858:253). in the original description of *Crotaphytus reticulatus*. states that it (*reticulatus*) is "more closely related to *Crotaphytus collaris* than to *Crotaphytus* (*Gambelia*) *wislizeni.*" These same words were repeated by Baird in 1959.[3] The use of *Gambelia* as a genus rather than as a subgenus for the leopard lizard was first applied by Smith in 1946. However, this was not widely accepted and Schmidt (1953:117) retained all species in the genus *Crotaphytus.* Robison and Tanner (1962) after examining the skeleton and the muscles of the pectoral girdle, throat, and head of *C. collaris*, *C. reticulatus* and *C. wislizeni*, were also opposed to the raising of *Gambelia* to full generic status. They found that many of the morphological differences existing between *collaris* and *wislizeni* are intermediate in *reticulatus* thus indicating a strong genetic, and, consequently, generic relationship between these three species. Although we believe that Baird's arrangement (i.e., *Gambelia* as a subgenus of *Crotaphytus* to include the leopard

2. Each of the above names, *wislizeni*, *gambeli*, and *fasciatus*, were described in the same volume of the same journal (Proceedings, Academy of National Sciences of Philadelphia, vol 6, on pages 69 (April), 126 (August), 207 (December), respectively.

3. Smith (1946:159) cites Baird (1857:7) as the original description of *Gambelia.*

lizards) should stand, further comparative consideration may be fruitful; we can not, however, pursue it further in this account.

The mutual and almost simultaneous recognition of this problem prompted us to unite our efforts toward an eventual major revision of this species complex. A start was made by comparing samples from the Great Basin with samples from the Upper Colorado River Basin and these in turn with samples from populations to the south. Such preliminary studies provided data which suggested a greater degree of variation in this species than has been previously indicated.

We are not yet prepared to present data covering all segments of the leopard lizard species complex. However, we have seen and examined most of the types (except *Crotaphytus* (*fasciatus*) *fasciolatus* Mocquard in the Paris Museum), particularly those types which effect our deliberations concerning populations occurring outside of Baja California. Within the United States, four subspecies of *Crotaphytus wislizeni* seem certain, but before we can determine the designations for the western populations certain nomenclatural problems must be resolved.

We have found that those populations occurring in the Rio Grande Valley of New Mexico and the Upper Colorado River Basin of Utah and Colorado present no major nomenclatural problems, and since both are very distinct, only these two populations will be considered in this report.

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E. Leviton, California Academy of Sciences (CAS); Dr. James R. Dixon, New Mexico State University (NMSU); and Dr. Frederick A. Shannon (FAS), Wickenburg, Arizona.

Genus *Crotaphytus* Holbrook

Subgenus *Gambelia* Baird

Crotaphytus wislizeni wislizeni Baird and Girard

Rio Grande Valley Leopard Lizard

(Figures 1 - 2)

Crotaphytus wislizenii Baird and Girard, 1852, Proceedings, Academy of Natural Sciences of Philadelphia, 6:69,[4] type locality, near Santa Fe, New Mexico; Baird and Girard, 1852, *in* Stansbury: 340-341, pl. 3.
Crotaphytus fasciatus Hallowell, 1852: 207-8.
Gambelia wislizeni wislizeni Smith, 1946:159.
Gambelia wislizenii wislizenii Cochran, 1961:105.
Crotaphytus wislizeni wislizeni (new combination) Schmidt, 1953: 117.

Type. USNM 2685. (See Remarks).

Range. Throughout the Rio Grande Valley of western Texas, northwestern Coahuila, northeastern Chihuahua, and central New Mexico, northwest to near the Utah-Arizona line, west through central and southern Arizona and northern Sonora to the Colorado River.

Diagnosis. Distinguished from all other *C. wislizeni* by several rows of large dark brown dorsal and lateral spots, each with a circle of white dots at or near the outer margin. In adults the light cross bands have faded or have developed into a series of small dots, often included as a part of the circular margin of the spots. The two median rows of brown spots are large, only one spot bebetween the dorsal cross bands and round to ovoidal in shape. Postmentals usually four but ranging from two to six.

Description of Subspecies. Scales on the body and head smooth, not imbricate; 30 to 50 dorsal, and all ventral scale rows enlarged; lateral scales small, beadlike; basal tail scales smooth, but becoming keeled and spined posteriorly; scales on dorsum of head only slightly enlarged and platelike; supralabials 12 (14.1) 16 [5]; infralabials 11 (13.85) 16; dorsals (parietal to base of tail) 179 (196.84) 223; scales at midbody 149 (167.8) 185; ventrals 90 (101.04) 117; femoral pores 18 (20.61) 25, each pore en-

4. Cope (1900, p. 255 cites the article in volume 6 of the Proceedings of the Academy of Natural Sciences of Philadelphia as the original description. However, beginning with the first edition of the check list of North American amphibans and reptiles by Stejneger and Barbour (1917) and continuing through all their editions (1923, 1933, 1939, 1943) the description in the Stansbury report is credited as the orginal. Smith and Taylor (1950), Schmidt (1953) and Cochran (1961) continued this erroneous usage. See discussion under *Remarks*.

5. Minimum range (mean in parentheses) maximum range.

tered posteriorly by one to three small scales; usually four postmentals, 2 (4.25) 6; gulars small and beadlike.

Head distinct, 22-30 mm. long (base of skull to snout) and 15-20 mm. wide; total length up to 400 mm.; snout to vent lengths 40 (recent hatchling) to 125 mm. in large adult; tail long, 65 to 70 per cent of total length; longest toe in adults (snout-vent of 100 mm. or more) 30 to 40 mm.

The color pattern consists of a juvenile and an adult phase. Both are distinct although variable, and will therefore be described separately.

Juvenile Pattern. A series of 7 to 9 well defined cream or white transverse bars occur in parallel sequence extending from the nape to the base of the tail; these bars may be straight, zigzag, or broken medially; dorsolaterally and laterally there are two series of white spots, often appearing as short bars, parallel or alternate

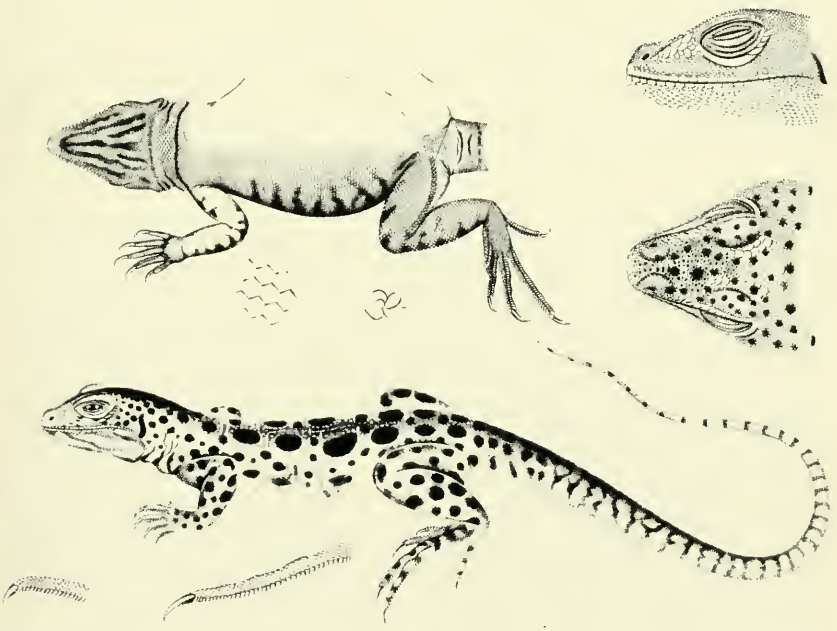

Figure 1. *Crotaphytus wislizeni wislizeni* showing the diagnostic dorsal pattern reproduced from plate 31 of Baird (1859). These drawings were listed as based on United States National Museum specimen 2685 by Baird (1859, p. 7) collected from "Sonora" by "Col. J. D. Graham, U. S. A." The caption from Baird (p. 35) states, "Plate XXXI. Figs. 1-8. - *Crotaphylus* (sic.) *wislizenii*, B. & G. No. 2685. - Fig. 1, animal; fig. 2, head from above; fig. 3, head from the side; fig. 4, inferior surface of body; fig. 5, a fore finger from the side; fig. 6, a hind toe from the side; fig. 7, dorsal scales; fig. 8, a femoral pore. All magnified, except figs. 1 and 4."

with dorsal bars; tail and hind legs also with white bars; white body bars one half to one millimeter long and encompassing 3 to 4 scales in a row; between the transverse bars, and lateral to mid-dorsal line, round brown spots form two rows of 7 to 9 spots on body; lateral spots of irregular size and position; dorsal spots occupy approximately one half of distance between transverse bars. On the posterior margins of white bars, two small dark half circular spots develop immediately anterior to large median spots becoming proportionately smaller in older juveniles and adults; in specimens ranging from 50 - 55 mm. in snout-vent length, a light circle forms around dark median spots; this light circle develops into a circular band of light dots in older lizards. The first adequate description of the juvenile pattern was provided by Ruthven (1907:516).

Adult Pattern. Transverse bars between nape and base of tail reduced in width to form narrow stripes, 1 to 2 scales across, or obliterated, usually irregular and confused with other light markings; dorsomedial dark spots large, usually occupying at midbody more than half of distance between transverse bars; usually four rows of smaller lateral spots, and one or two small spots between large medial spots and anterior transverse bar. Around each of spots, medial and usually in the first two or three lateral rows of spots, a conspicuous circle of small white dots (2 to 4 scales in each dot) occur at or near the outer edge; head and tail spots not so encircled; transverse white bars often forming a portion of dotted circles and tending to become more obscure. Ground color grayish brown, light to medium brown or dark brown; ground color variable, reflecting age and population differences.

Specimens Examined. A total of 96 as follows: *ARIZONA*: *Cochise County*: 0.9 miles Southwest of Portal (MVZ) 67023); 31 miles Southwest of Portal (MVZ 6707;). *Gila County*: Gila River (USNM 22130). *Maricopa County*: 2 miles Southwest of Morristown (FAS 6701); 0.75 miles north of Morristown (FAS 6748); Paradise Valley (CAS 17238); 1.5 miles Southwest of Wickenburg (FAS 1355, 1496 and 7502); 3.5 miles Southwest of Wickenburg (FAS 1456); 9 miles West of, 4 miles North of Wickenburg (FAS 12314); Divide, 11 miles West of Wickenburg (FAS 12772); Winter's Well, 15 miles Northwest of Palo Verde (USNM 1474-5). *Mohave County*: Dolan's Spring (MVZ 16020); 0.5 miles West of Hackberry (FAS 7359-61); 7.6 miles north of Wickieup (FAS 16023). *Pima County*: Santa Catalina Mountains (CAS 34320); 9 miles south of Ago (FAS 4849); Tucson (USNM 17180, 19698, FAS 276); Turner's Tanks (USNM 60106); no specific locality (USNM 61378). *Yavapai County*: 10 miles northeast of Aguila (FAS 3008, 15612 and 15614); 9.8 miles northwest of Congress (FAS 11590); 6 miles northwest of Wickenburg (FAS 3442). *Yuma County*: Papago Wells (CAS 34204-8); Yuma (CAS 33486 and 33490).

NEW MEXICO: *Bernalillo County*: Albuquerque (SU 11798-11801; USNM 37961, 38054, 58304-5). *Dona Ana County*: *Las* Cruces (USNM 22267, NMSU 1489 and R-9); College Ranch near Mexico (NMSU R-3 and R-63); Red Lake, 41 miles north of Las Cruces (NMSU 271-2); 7 miles north of Hwy. 80 (NMSU 1488); 5.5 miles north of Radium Springs (NMSU 2047); 1.4 miles west of Intersection Hwy 359 (NMSU 1487). *Hidalgo County*: Hachita USNM 45067 and 45105); 27 miles north of Rodeo (MVZ 67164). *Luna County*: 0.5 miles east of Columbus (CNHM 51771); Deming (USNM 44956). *Santa Fe County*: near Santa Fe (USNM type and 8475). *Valencia County*: near Grants (SU 5043-4); Laguna (USNM 4274).

TEXAS: *El Paso County*: El Paso (CAS 74036). *Hudspeth County*: Ft. Hancock (USNM 20668); 7 miles southwest of McNary (NMSU 2070). *Reeve County*: 20 miles east of Toyahvale (USNM 32843-4); Pecos River (USNM 5064).

MEXICO: *Chihuahua*: 1 mile south of Ahumada (USNM 104738-40); 6 miles southwest of Rancho Maria (USNM 10471); Rancho Maria, Near Progresso (USNM 104741-50); Santa Maria (CNHM 1639); Lake Santa Maria (USNM 47414); no specific locality (USNM 58036). Sonora: 5 miles northeast of Libertad (CM 4810); northwestern Sonora (USNM 2685 and 431830); Tiburon Island, Gulf of California (SU 17049-50; USNM 64464).

Figure 2. Dorsal view of type specimen of *Crotaphytus fasciatus* (USNM) 2736) showing its dorsal pattern identical to *Crotaphytus wislizeni wislizeni*.

Remarks: The original description of this species first appeared as a short preliminary note in April, 1852, and is quoted in its entirety as follows:

"*CROTAPHYTUS WISLIZENII*, B. and G. — Head proportionally narrow and elongated; cephalic plates and scales on the back very small; yellowish, brown, spotted all over with small patches of deeper brown or black. Caught near Santa Fe, by Dr. Wislizenius (sic.); specimens of the same species sent in by Lieut. Col. L. D. Graham, collected between San Antonio and El Paso del Norte."

At the beginning of the article containing this description is the following statement: "Full description and figures of these species will shortly appear in Capt. Stansbury's Report to Congress on the great (sic.) Salt Lake (Utah)." As previously stated, Cope (1900:255) was obviously correct in assigning the original description to the April 1852 Proceedings article. The more detailed account in the Stansbury report followed several months later.

The description in the Stansbury Report (1852:340) is general and basically concerned with body proportions and color pattern differences between *C. collaris* and *C. wislizeni*. Although one of the basic dorsal color pattern differences in *wislizeni* is not included in the original description, Baird (1859, plate 31) does show the circle of white spots surrounding each of the large brown spots. This is based upon a specimen from "Sonora," Mexico, (see figure 1 which we have designated as the lectotype). This character was later recognized, in part at least, and reported in the description of *Crotaphytus gambeli* by Baird and Girard in August 1852:126 as follows: "The general distribution of color is the same as in C. *wislizenii;* the only difference consists in the absence of the small yellowish white dots spread all over the body of the latter species. The transverse yellowish markings appear also to be more conspicuous."

There is a question as to whether or not the designation of USNM 2770 is correct. Cochran (1961:105) was apparently aware of this problem as she quoted the following from the "original description:" "Figured specimen caught near Santa Fe, New Mexico, by Dr. Wislizenus." This is a misquote, and should correctly read, "Caught near Santa Fe, by Dr. Wislizenius." Dr. Wislizenus' name was misspelled in the original description and the misspelling was not listed on the "Errata in Vol. VI" of the Proceedings of the Philadelphia Academy. In the more detailed description that appeared later in the Stansbury Report, the name was spelled correctly stating, "The specimen which we have figured was caught near Santa Fe, by Dr. Wislizenus, during the Mexican War." The holotype of *Crotaphytus wislizeni* is listed by Yarrow (1882:53); Cope, (1900:258); Smith and Taylor (1950:94); Cochran (1961:105) as USNM 2770, collected at "Colorado" by H. Baldwin Möllhausen, no date given. Möllhausen was one of two naturalists (the other being Dr. C. B. R. Kennerly) attached to the survey of the

Pacific Railroad Route, under the command of Lt. A. W. Whipple in 1853-1854, (after *C. wislizeni* was described). Yarrow (1882:53) apparently was the first to designate holotypes for the United States National Museum collections and the designation of USNM 2770 as the type must be attributed to him.

The type mentioned, but not designated by Baird and Girard, as obtained by Dr. Wislizenus has presumably been destroyed, according to a recent letter from Dr. Doris M. Cochran. This animal must have been collected around the end of June or early July of 1846. We have checked Wislizenus' account (1848) of his

Figure 3. Dorsal view of the adult pattern of *Crotaphytus wislizeni wislizeni* based upon a specimen from Cochise County, Arizona.

journey across New Mexico, Texas, and Chihuahua, and were unable to find any reference to the specific collection of any reptiles, let alone of a leopard lizard. Since no type specimens were designated in the original and subsequent descriptions, and since the allusion to the specimen obtained by Möllhausen is an obvious error, we must of necessity designate another type specimen. In the original description Baird and Girard stated, "specimens of the same species sent in by Lieut. Col. J. D. Graham, collected between San Antonio and El Paso del Norte." Baird (1859, plate 31) was

the first one to actually show the dorsal color pattern of *C. w. wislizeni* based upon USNM 2685 from "Sonora" obtained by "Col. J. D. Graham, U.S.A." Because this specimen is still available in the collections of the United States National Museum and owing to the fact that specimens from "between San Antonio and El Paso del Norte" obtained by Colonel Graham were mentioned in the original description, we take the liberty of designating USNM 2685 as the holotype for *C. wislizeni wislizeni*. This is necessitated by the fact that the allusion to the specimen obtained by Möllhausen, USNM 2770 as the type, is an obvious error.

We are aware of the problems involved in specifically designating localities listed by the early survey reports. Areas included in Sonora, Utah, etc., do not have the same boundaries today. It is common knowledge that the names of many areas have been changed with the advance of history and what was once alluded to as "Sonora" in the 1850's may now be portions of New Mexico, Arizona, Chihuahua or Sonora. Although the state of Sonora, Mexico, as it is now constituted, is included in the range of *Crotaphytus w. wislizeni*, it is questionable that any of the type series used by Baird and Girard were actually collected in Sonora as recognized today.

Other studies (Van Denburgh, 1922, pl. 8; Smith 1946, p. 160, pl. 30) have shown the color pattern as described above, but seemingly have not recognized its significance. Ruthven (1907, p. 516) perhaps came closest to describing the pattern of the circle of white dots around the darker and larger spots in specimens of *Crotaphytus wislizeni wislizeni* from Alamogordo, New Mexico, and Tucson, Arizona, than any previous author. (Fig. 3).

Crotaphytus wislizeni punctatus, new subspecies

Small Spotted Leopard Lizard

(Figures 4-5)

Type. An adult female, BYU 20928, taken in the Yellow Cat mining District approximately 10 miles south of U.S. Highway 50-6, Grand County, Utah, by Wilmer W. Tanner on 28 June 1961.

Paratypes. *COLORADO*: *Mesa County*: Grand Junction (USNM 44793-5). *UTAH*: *Emery County*: approximately 15 miles northwest of Hanksville (BYU 16497 and 20931-3); Green River (CAS 38376); 25 miles northwest of Hanksville (BYU 14913); 5 miles west of Temple Mountain Junction (BYU 20934-9; CAS 92466-9 and 93358). *Garfield County*: Star Spring (BYU 12846); one mile east of Star Spring (BYU 11742 and 12187); mouth of North Wash (BYU 12558); Trachyte Creek at Junction of Utah Highway 95 (BYU 12614-17); six miles south of Wayne-Garfield county line on Utah Highway 95 (BYU 12685). *Grand County*: 10 miles south of Cisco (BYU 12857, 12859-600); Castle Valley (BYU 12853); Moab (BYU 11363); Arches National Monument (BYU 9040-1, 10243 and CM 20765-6, CNHM 62810); Yellow Cat Mine

(BYU 20610 and 20920-30); Thompson (CAS 38217-34, 41131, 41133-5); Elgin (CAS 38343-4); *Kane County*: Hall Cave (BYU 122, 924-8); 15 miles northwest of Hole-in-the-Rock (BYU 11271); Lone Rock (BYU 11325, 12008 and 14981); Willow Spring tank (BYU 114); Catstare Canyon (BYU 11347-8, 11329-30, 11378-81, 12186, and 12873); Crossing of the Fathers (BYU 14912). *San Juan County*: Bluff (BYU 482); Navajo Mountain Trading Post (BYU 12554); Green Water Spring (BYU 16751); Montezuma Creek (BYU 16797-8); Copper Canyon, 3 miles north of old mine (MVZ 21792). *Wayne County*: Hanksville (BYU 8396-7).

Other Material. *ARIZONA*: *Coconino County*: Wahweap Creek (MVZ 21793); one mile west of Glen Canyon Dam (BYU 18920); 16 miles west of Marble Canyon Bridge (MVZ 16383); Marble Canyon (BYU 556); Tuba City (BYU 555 and MVZ 8663). *Navajo County*: Joseph City (BYU 12782-3). *UTAH*: *San Juan County*: two miles above mouth of Nokai Creek (CNHM 37419). *Sevier County*: two miles south of Joseph (MVZ 49711-2). *Washington County*: Ivans (BYU 6801); Saint George (BYU 515 and 1635).

Diagnosis. Similar in habits to other adjacent populations of *Crotaphytus wislizeni* but distinct in having a dorsal color pat-

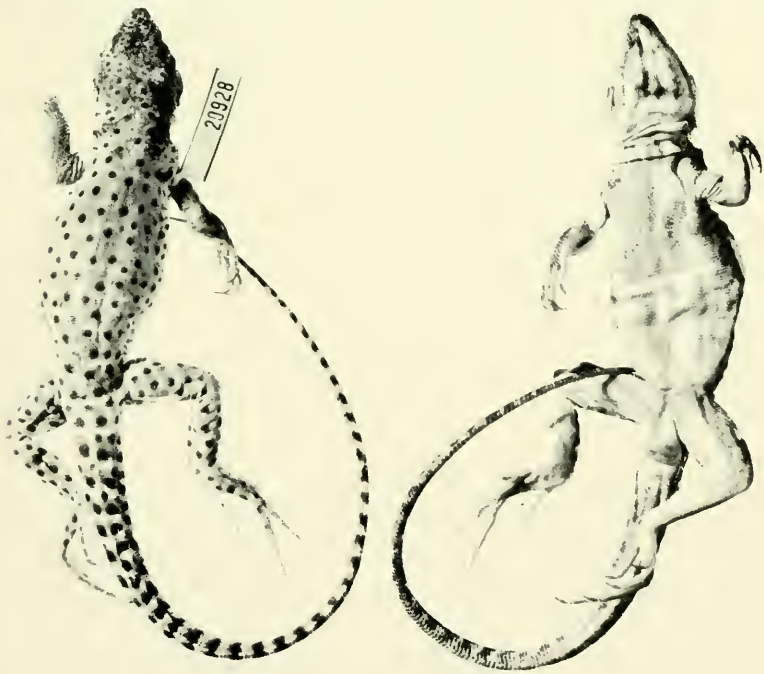

Figure 4. A. Dorsal view of holotype of *Crotophytus wislizeni punctatus*. (BYU20928). B. Ventral view of holotype.

tern of numerous, small, round brown spots on a background of light brownish gray and with the transverse bars reduced to narrow or faint lines in adults. In contrast to some populations occurring in the Great Basin and Baja California to the west and southwest, to all *C. w. wislizeni* in Arizona, New Mexico and northern mainland Mexico, the dorsal brown spots are not encircled by white or cream colored spots at or near their margins. Only a limited degree of dorsal pattern polymorphism seems to occur. (see fig. 5). Furthermore, *C. w. punctatus* is distinct from all other subspecies in having an increase in postmentals from 4 to 6. (see fig. 6).

Description of Type. An adult female, snout vent 104.5, total length 309.5 mm., tail into total length .6624; orbit to rostral 8.3; orbit to ear 9.2; dorsal scales (occipital scale to base of tail) 212; ventrals 102, noticeably larger than laterals and dorsals; scales around middle of body 175; middorsal rows only slightly enlarged, beadlike; supralabials 17-18; infralabials 15-16; femoral pores 22-23; one to three usually two, small scales contacting pores posteriorly; dorsal head scales from rostral to occiput 22; postmentals 4 right side, 3 left side, 7 total; scales on anterior half of tail smooth, posteriorly keeled but not spinous. Head scales smooth and platelike, some raised medially, none imbricate; gular scales elongate anteriorly, becoming rounded and beadlike before and at the gular fold; ventrals enlarged, imbricate and in approximately 35 longitudinal rows.

Head distinct, 24.8 mm. long, 20.5 wide; body slightly flattened, wider than high; longest toe 20.0 mm. Color pattern consisting of a series of nine transverse bars from neck to base of tail, greatly faded, not distinct anteriorly; dorsal and lateral spots small, involving 7 to 16 scales; 10 to 12 spots on one side between two transverse bars; lateral spots smallest, tail with two dorsal and two lateral rows of spots, larger than body spots and becoming progressively larger posteriorly until they fuse to form black and white rings; gular region marked with seven parallel dark stripes extending from labials to near gular fold where they terminate; dorsum of hind legs spotted and colored as body; front legs with gray body color but without spots; body ground color gray (see remarks); brown spots distinct.

Range. Upper Colorado River Basin in Utah from Uintah County through Emery to Kane and Washington counties on the west and south; southeast through western Colorado to northwestern New Mexico and west along the northern edge of Arizona (north of the Little Colorado and the Colorado River at least to Toroweap in Mohave County).

Remarks. The dorsal pattern in the subspecies of *C. wislizeni* appears to have four important variables in the adults: (1) the general background color; (2) number and size of dorsal dark

spots; (3) the size of the dorsal transverse bars; and (4) the presence or absence of other dorsal markings such as the fine light dots surrounding the brown spots in *C. w. wislizeni.*

Based upon the three subspecies now recognized the following remarks are appropriate. The background color is lightest in *C. w. punctatus* and darkest in *C. w. silus.* In the latter the scales are mostly dark brown or tending toward black, but in *C. w. wislizeni* there are lighter shades and a tendency for the base of each scale (not included in a brown spot) and the skin between scales, to be much lighter than the crown. In *C. w. punctatus*, this is carried still further in some specimens with only the top of each scale pigmented. This produces a blending or fusion of the basal white and

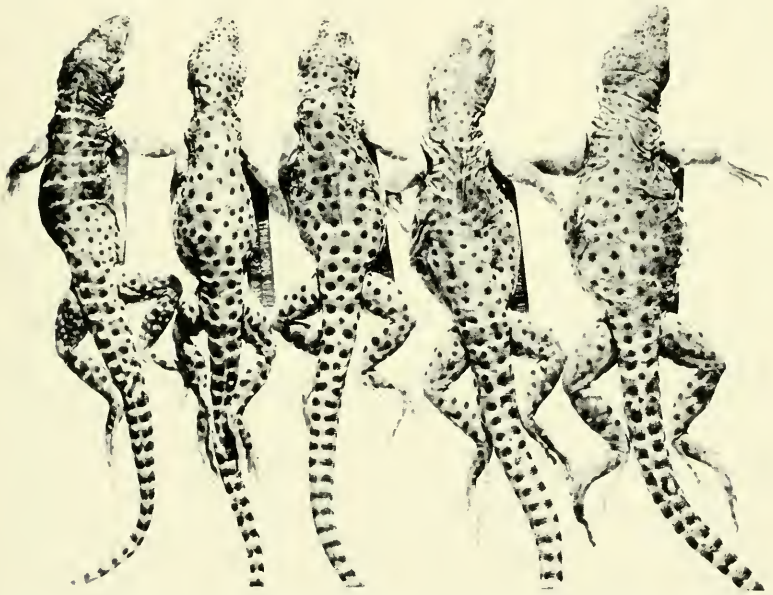

Figure 5. The limited range of dorsal pattern polymorphism of *Crotaphytus wislizeni punctatus* as indicated by a portion of the paratypic series from Thompson, Grand County, Utah.

the dark dot on the crown of each scale into a gray or brownish ground color. This factor, in addition to (or combined with) the size of the dorsal spots, determines in a general way whether the lizard will have a dark (*silus*) or light (*punctatus*) appearance. The light colored appearance of other segments of the Upper Colorado River herpetofauna was first commented upon by Van Denburg (1922).

The number of spots is perhaps not as variable as their size, although in *punctatus* the spots are not only smaller but also more numerous than in *wislizeni.* A comparison of *wislizeni* with specimens from Nevada and California, including *silus*, indicates that

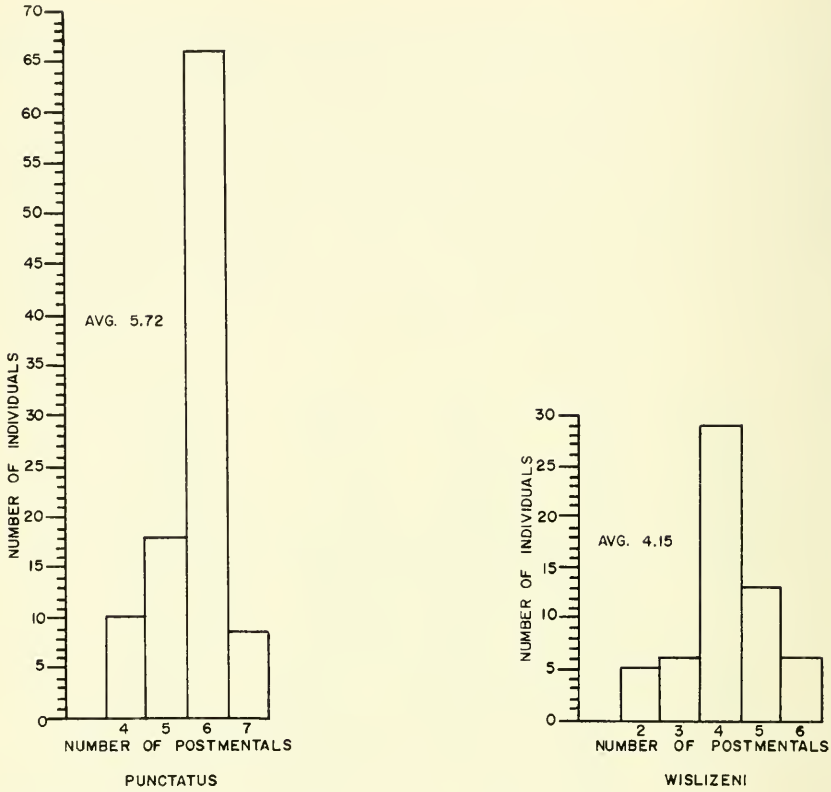

Figure 6. Histograms showing the numbers of postmentals in A., *C. w. wislizeni* and B, *C. W. punctatus.*

the size of spots rather than the number of spots is the variable. This is also generally true for the transverse bars, with *silus* having wide distinct bars and the eastern subspecies, *punctatus* and *wislizeni*, narrow, faint (even to forming a discontinuous series of dots), to a complete absence of the bars in old adults.

Perhaps the most ornate character in the dorsal pattern is the development of the circle of white dots around the dark rust brown spots. (Those having this character well developed, are, in our opinion, one of temperate North America's most attractive and beautiful lizards). This character is present in *C. w. wislizeni* as we have defined it and has been observed in specimens from northern Baja California (San Andreas), southern California and extreme south and eastern Nevada. It may, therefore, be necessary to extend the range of *C. w. wislizeni* to these areas as additional material indicates more adequately the extent of the actual geographic ranges.

Specimens of *C. w. punctatus* from central Sevier County, Utah, represent the only known records outside of the Colorado

River Basin. Their occurrence here is not surprising for it is known that other reptile species (e.g., *Sceloporus undulatus elongatus*) have penetrated the eastern margins of the Great Basin, presumably through Salina Canyon.

Specimens seen from Washington County, Utah, are also *punctatus;* however, a few specimens from the western part and north along the Nevada line to Iron County show traces of the white dots (see Van Denburgh 1922b, plate 8). There is also a reduction in the postmentals with four being most common.

Intergradation between *C. w. punctatus* and *C. w. wislizeni* also appears to occur in central Coconino County, Arizona. Specimens from the Tuba City-Cameron area show faint but definite tracings of the white circle of dots around the dark spots, but have six postmentals and small spots and are considered to be closer to *C. w. punctatus.*

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NEW LACEBUGS FROM THE EASTERN HEMISPHERE

Carl J. Drake[1]

The present paper describes six new species, two from the Philippines, two from Rhodesia, one from Jordan, and one from the Ivory Coast. Unless recorded otherwise, beneath the description, the types are in the Drake Collection (USNM). The author desires to express his sincere appreciation to Miss Liza Biganzoli, Washington, D.C. for the fine illustrations.

Cysteochila pelates, new sp.

Figure 1

Small, oblong, brown with head black and cephalic spines testaceous; body beneath with abdomen dark brown and thoracic sterna blackish. Legs reddish brown with tibiae testaceous. Antennae with segments I and II brown, III testaceous, IV swollen apically and mostly dark fuscous. Length 2.75 mm., width 0.80 mm.

Head very short, armed with five short spines; labium reaching middle of mesosternum, sulcus open behind. Antenna slender, indistinctly pilose, measurements: segment I, 0.11 mm.; II, 0.10 mm.; III, 0.70 mm.; IV, 0.20 mm. Pronotum moderately convex, coarsely punctate, tricarinate. All carinae raised and non-areolate; median carina percurrent; lateral pair concealed in front of middle of disc by reflexed paranota, divergent posteriorly behind pronotal disc; collar slightly raised at middle so as to form a small tectiform hood; paranotum totally reflexed, covering anterior part of lateral carinae, six areolae deep in widest part; posterior triangular projection finely areolate.

Metathoracic scent glands with ostiole and ostiolar sulcus on each metapleuron, the sulcus nearly vertical. Legs short, with femora slightly swollen, indistinctly pubescent. Elytra scarcely wider and only a little longer than abdomen, finely areolate, with sutural area on same horizontal plane as discoidal area; costal area absent; subcostal area narrow, vertical, biseriate; discoidal area large, acutely angulate at base and apex, five areolae deep opposite apex of hind projection of pronotum, acutely angulate at base and apex; sutural areas overlapping with apices jointly rounded. Hind wings as long as abdomen.

Holotype, macropterous ♂, Aquaba, Jordan, 3.V.1963, on *Acacia segal* Del., collected by Dr. Hans Eckerlein. One paratype ♂, same data as type, in Eckerlein Collection. The holotype is illustrated.

The small form, closely reticulated dorsal surface, and obsolete costal areas separate this little species from its congeners.

1. Smithsonian Institution, Washington, D. C.

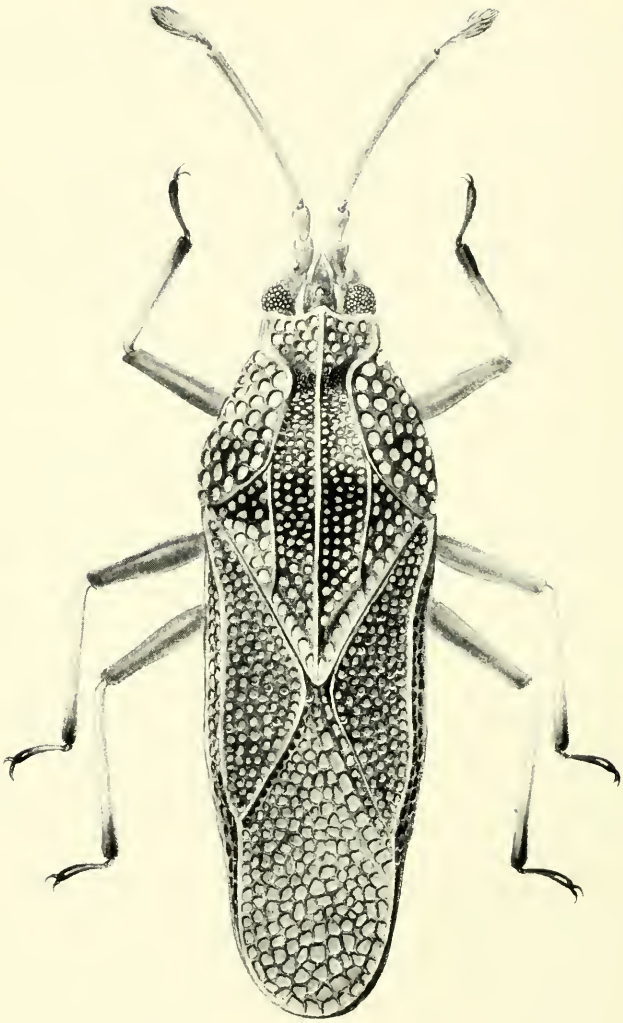

Fig. 1. *Cysteochila pelates*, new sp.

Cysteochila apheles, new sp.
Figure 2

Small, oblong, whitish testaceous with head dark brown; pronotal disc, posterior half of paranota, apex of backward projection of pronotum, median carina on pronotal disc, crossband on elytra (including most of discoidal area), apical part of costal area, and entire sutural area brownish fuscous; bucculae brown with hind margin testaceous; body beneath reddish brown. Sternal laminae

of rostral sulcus testaceous, rostrum brownish. Antennae brown, with third segment brownish testaceous. Legs with coxae, trochanters, and basal three-fourths of femora reddish brown, the apices of femora and tibiae testaceous. Hind wings clouded with fuscous. Length 2.50 mm.; width (elytra) 0.90 mm.

Head very short, armed with five testaceous spines, anterior three spines porrect and hind pair appressed; eyes large, dark fuscous; bucculae wide, areolate, closed in front. Antenna slender, moderately clothed with extremely short golden pubescence,

Fig. 2. *Cysteochila apheles*, new sp.

measurements: segment I, 0.11 mm.; II, 0.10 mm.; III, 0.64 mm.; IV, 0.32 mm. Rostrum extending to base of mesosternum; laminae of sulcus uniseriate; channel narrow, parallel on prosternum, slightly wider and feebly divergent on mesoternum, much wider and cordate on metasternum, closed behind. Ostiole and ostiolar canal present on each metapleuron, channel almost vertical, the sides elevated.

Pronotum moderately convex, punctate, areolate on backward projection, tricarinate; median carina slightly more raised than lateral pair, slightly higher, arched and clearly uniseriate on pronotal disc; lateral carinae barely concealed by reflexed paranota on pronotal disc, divergent posteriorly on triangular process. Hood small, low, extending backwards between calli, slightly produced in front; paranota very large, reflexed, feebly elevated opposite humeral angle. Legs moderately long; femora little swollen, sparsely clothed with short golden pubescence.

Elytra not much wider and scarcely longer than abdomen; sutural areas overlapping each other with apices jointly rounded in repose; costal area moderately wide, composed of two rows of serially arranged areolae; subcostal area slightly narrower than costal area, biseriate, gently sloping downwards; discoidal area large, two thirds as long as elytra, acutely angulate at base and apex, widest just behind middle, there five or six areolae deep. Hypocostal ridge uniseriate, areolae small.

Holotype, macropterous ♂. San Jose, Mindora, Philippine Islands, C. F.Baker.

Closely allied to the species described below, but easily separated from it by the pale testaceous color and prominent fuscous markings, longer antennae, and arched median carina on pronotal disc. The holotype is illustrated.

Cysteochila aei, new sp.
Figure 3

Small, oblong, reddish brown with basal part of costal area up to and then beyond median crossband to clouded apex brownish testaceous; body beneath brown, shiny. Legs brown with tibiae brownish testaceous. Antenna brown with third segment brownish testaceous and fourth fuscous. Length 2.50 mm.; width 0.95 mm.

Head very short, armed with five brown spines, anterior three spines porrect, hind pair appressed; eyes large, dark fuscous; bucculae very wide, areolate, closed in front. Rostrum extending to end of mesosternum, rostral laminae badly broken. Antenna slender, rather sparsely clothed with inconspicuous, golden pubescence, measurements: segment I, 0.10 mm.; II, 0.09 mm.; III, 0.75 mm.; IV, 0.34 mm. Ostiole and ostiolar channel of scent glands present on each metapleuron. Legs slender, femora slightly swollen.

Pronotum moderately convex, punctate, tricarinate; median carina more elevated on pronotal disc, there distinctly uniseriate,

Fig. 3 *Cysteochila aei*, new sp.

areolae becoming indistinct on backward projection of pronotum; lateral carinae concealed on pronotal disc by reflexed paranota, indistinctly areolate, slightly divergent posteriorly on triangular process; paranota very large, reflexed, just covering lateral carinae, feebly elevated adjacent to humeral angles. Elytra with sutural areas overlapping each other with apices overlapping and jointly rounded in repose; costal area moderately wide, composed of two rows of areolae; subcostal area slightly narrower than costal area; nearly vertical, biserate; discoidal area large, extending beyond mid-

dle of elytron, acutely angulate at base and apex, widest behind middle, there five or six areolae deep; sutural area on same horizontal level as discoidal area. Hind wings not as long as fore pair, densely clouded with fuscous.

HOLOTYPE, macropterous ♂, Montalban, Luzon, Philippine Islands, C. F. Baker.

The largely brown dorsal surface, brown femora, tectiform hood, and less elevated median carina on pronotal disc, separate this species from *C. apheles*.

Cysteochila epelys, new sp.
Figure 4

Oblong, wide, pale brown with head, hood, pronotum (except hind projection), rear half of each paranotum, pronotal carinae, median and subapical crossbands of elytra blackish fuscous; body beneath brown with mesosternum black; sternal laminae of rostral sulcus brownish testaceous. Legs with basal three-fourths of femora reddish brown, tips of femora, tarsi and most of tibiae flavotestaceous. Antenna with segments I and II dark brown, III brownish, IV dark fuscous. Length, ♂ and ♀ 4.20 mm.; width ♂ 1.25 mm.; ♀ 1.35 mm.

Head short, armed with five short testaceous spines; bucculae areolate, closed in front. Antenna moderately long, slender, inconspicuously clothed with short golden pubescence, measurements: segement I, 0.15 mm.; II, 0.10 mm.; III, 0.90 mm.; IV, 0.38 mm. Labium brown, reaching to metasternum; sulcal laminae wide, uniseriate, parallel on mesosternum, more widely separated and cordate on metasternum, open behind.

Pronotum wide, moderately convex, coarsely pitted, tricarinate, each carina uniseriate; median carina more elevated than lateral pair, highest on pronotal disc; lateral carinae divergent posteriorly, concealed on pronotal disc by reflexed paranota; hood moderately large, inflated, somewhat pyriform, produced backwards behind calli on anterior part of pronotal disc; paranotum very large, reflexed, resting on lateral carina, three rows of cells deep in upright part and seven or eight in reflexed part; thoracic scent glands with ostiole and sulcus on each metapleuron, sulcus vertical with sides raised.

Elytra a little wider and longer than abdomen, sutural areas overlapping each other in repose; costal area wide, composed of two rows of moderately large areolae, the areolae clear except in crossbands; subcostal area narrow, vertical, composed of two rows of small, rounded areolae; discoidal area large, five-eighths as long as elytron, four or five cells deep in widest part, acutely angulate at base and apex; sutural area large, on same level as discoidal area, with areolae fairly large and subequal in size to those in discoidal area. Hind wings clouded with dark fuscous.

HOLOTYPE, macropterous ♂, Abijan, Ivory Coast, French West

Fig. 4. *Cysteochila eyplys*, new sp.

Africa. Jan. 1962. E. Laborve, in Paris Museum (fig. 4). ALLOTYPE, macropterous ♀, same data as type, Drake Collection (USNM).

The broad form, shape of hood, and coloration distinguish *epelys* from its congeners described here.

Cysteochila cybele, new sp.

Oblong, rather broad, brown, without markings on reticulated surface; head blackish with dorsal spines testaceous; body beneath brown with mestosternum blackish. Antennae brown with fourth segment swollen and mostly black. Legs yellowish brown with fe-

mora tending to be darker. Length 3.10-3.25 mm., width (middle of elytra) 1.62 mm. Female usually slightly broader and more obovate than male.

Head very short, armed with five long spines, anterior spines porrect, basal pair recumbent; bucculae wide, areolate, closed in front. Rostrum extending to base of mesosternum; laminae of rostral sulcus uniseriate, with sulcus narrow and sides parallel on mesosternum, wider and cordate on metasternum, ends of laminae forming a v-shaped opening behind. Antenna slender, indistinctly pubescent, fourth segment subclavate, measurements: segment I, 0.12 mm.; II, 0.10 mm.; III, 0.72 mm.; IV, 0.25 mm. Legs rather short, indistinctly pubescent, femora only slightly swollen.

Pronotum broad, moderately swollen, rugulosely punctate, tricarinate, all carinae raised, distinct, and non-areolate; median carina percurrent; lateral pair completely concealed on pronotal disc by reflexed paranota, divergent posteriorly on backward extension; hood very small, testiform, feebly projected forward at middle; paranotum large, totally reflexed, extending inward slightly farther than lateral carina, moderately clothed on lateral sides by fine grayish hairs. Ostiole and ostiolar canal of metathoracic scent glands very distinct on each metapleuron, with channel vertical and sides raised.

Elytra wide, with sutural areas overlapping each other so that their apices lie jointly rounded at rest, not much longer than abdomen; costal area moderately wide, composed of one to almost two complete rows of areolae, usually with outer row complete and a partial inner row in basal third of area; subcostal area mostly biseriate, nearly vertical, not as wide as costal area; discoidal area large, almost three-fourths as long as elytron, with areolae somewhat irregular and confused in arrangement, seven or eight cells deep in widest part just behind middle; sutural area large, on same horizontal level as discoidal area, areolae slightly larger than those in discoidal area. Hind wings slightly shorter than front pair, clouded with fuscous.

Holotype, ♂ and allotype, ♀, both macropterous, 30 miles northeast of Kapar Mpashi, Northern Rhodesia, 9.V.1956, C. N. Smithers. *Paratypes*: 9 specimens with same data as type.

The broader form, solid brown color, wider and hairy sides of pronotum distinguish this species from its congeners described herein. The costal area varies slightly in width and ranges all the way from one to two full rows of areolae.

Leptopharsa ralla, new sp.

Very elongate, moderately widening posteriorly, widest across apices of elytra, brownish testaceous with head, eyes and calli dark fuscous; antennae testaceous with fourth segment almost entirely blackish fuscous; legs testaceous with tips of tarsi blackish. Body beneath brownish fuscous with rostral laminae whitish testaceous.

Length 3.70 mm.; width 0.75 mm. (pronotum) and 1.09 mm. (across apices of elytra).

Head very short, slightly produced in front of eyes, armed with five testaceous spines; three frontal spines short, tubercular; hind pair long, appressed, extending forward to front margin of eyes; bucculae wide, areolate, closed in front. Labium moderately long, testaceous, extending to base of mesosternum; rostral laminae

Fig. 5. *Stephanitis subfasciata* Horváth.

uniseriate, closed at base, the areolae moderately large. Antenna very long, about five-sevenths as long as entire insect, measurements: segment I, 0.32 mm.; II, 0.11 mm.; III, 0.80 mm.; IV, 0.38 mm. Ostiole and ostiolar canal of metathoracic scent glands present on each metapleuron.

Protonum moderately convex, punctate, tricarinate; lateral carinae slightly raised, slightly divergent anteriorly, indistinctly areolate; median carina slightly more raised than lateral pair, percurrent, areolae a little larger and clearly visible in front of middle of pronotal disc, the cells between calli fairly large; collar raised, composed of two rows of areolae, without any indication of pronotal hood; paranotum moderately wide, wider in front than behind, composed of a single row of areolae; posterior process of pronotum long, triangular, blunt at apex. Legs very long, slender; femora not swollen.

Elytra narrow, very little wider but much longer than abdomen; costal area composed of one row of fairly large areolae; subcostal area narrow, nearly vertical, mostly biseriate; discoidal area elongate, acutely angulate at base and apex, widest near middle, there four areolae deep, not quite reaching middle of elytron, sutural areas large, overlapping each other. Hind wings extending a little beyond apex of abdomen, not as long as elytra.

Holotype, macropterous ♂, Chirinda Forest, South Rhodesia, 6-8.VIII. 1957, C. N. Smithers. The elongate form, very long legs, and very long antennae separate this species from African members of the genus. The antennae are five-sevenths as long as the entire length of the body.

Stephanitis subfasciata Horváth
Figure 5

Stephanitis subfasciata Horváth 1912, Ann. Mus. Nat. Hungarici, vol. 10, pp. 320, 325.

This species was originally described from China (Macao) and Formosa (Takao). We have specimens from the type localities (det. Horváth) plus other material from Java, Larat Island, Hong Kong, and China (Foochow). The specimens from Larat have the veinlets of hood and dorsal surface mostly reddish brown instead of pale testaceous. A specimen from Larat is illustrated.

UNDESCRIBED SPECIES OF NEARCTIC TIPULIDAE (DIPTERA). III.

Charles P. Alexander[1]

At this time I am characterizing various species of the genus *Tipula* Linnaeus, derived from several sources, as follows: Two species from California, discovered during the progress of a survey of the cave fauna under the leadership of Mr. Richard E. Graham, in collaboration with Dr. Willis J. Gertsch and Mr. R. de Saussure; two further species from Maine and Newfoundland, taken by Mr. David L. Carson and Dr. A. E. Brower; and a further very interesting crane fly discovered by Mr. James Baker in the Steens Mountains, Oregon. The disposition of the type specimens and further acknowledgements are indicated in the text.

Tipula (*Trichotipula*) *gertschi*, n.sp.

General coloration of mesonotum dark brown, praescutum with four obscure brownish yellow stripes; antennae of male relatively long, flagellum dark brown; claws of male simple; wings faintly darkened, stigma darker brown; macrotrichia in outer fourth of cell R_5; no stigmal trichia; abdominal tergites dark brown, bases restrictedly more yellowish; male hypopygium with tergal lobes entirely without blackened spicules, ninth sternite with two pencils of long black setae, inner dististyle with lower beak blackened.

Male. Length about 8 mm.; wing 9 mm.; antenna about 3.9 mm.

Female. Length about 12 mm.; wing 11.5 mm.

Frontal prolongation of head short and stout, the nasus virtually lacking; dorsum brownish yellow, sides brownish black, midventral area pale; palpi dark brown, terminal segment elongate, brownish yellow. Antennae of male relatively long; scape and pedicel slightly paler than the dark brown flagellum; flagellar segments subcylindrical, the basal enlargements feebly indicated, verticils shorter than the segments; terminal segment very small, globular, about one-third the verticils. Head medium brown.

Pronotum obscure yellow, scutum restrictedly patterned with pale brown. Mesonotal praescutum brown with four obscure brownish yellow stripes, the intermediate pair slightly broader than the dark median interspace, the latter narrowed to a point behind, very narrow in the type; posterior sclerites of notum dark brown, with vague indications of a capillary median paler vitta extending from suture to abdomen. Pleura brown, dorsopleural membrane whitened. Halteres infuscated, base of stem narrowly yellowed. Legs with coxae pale brown basally, apices restrictedly paler; tro-

1. Amherst, Massachusetts.

chanters yellow; remainder of legs medium brown; claws simple. Wings faintly darkened; stigma oval, darker brown; restricted obliterative areas before stigma and across base of cell *1st* M_2; pale longitudinal lines in cell *1st A* and outer end of *R*; veins light brown. Macrotrichia in outer fourth of cell R; no stigmal trichia; medial veins chiefly glabrous, trichia present on most of M_1, outer end of M_2 and in cases at tip of M_3. Venation: *Rs* shorter than *m-cu*; petiole of cell M_1 about one-half longer than *m*.

Abdominal tergites dark brown, proximal ends restrictedly more yellowed; sternites light brown, their posterior borders narrowly yellowed. Male hypopygium with posterior border of tergite having a broad U-shaped emargination to form relatively narrow obtuse lobes, margins of the latter entirely without spicules or spinoid setae, as in other species, having numerous very small and delicate setae only. Ninth sternite on either side with a brush or stout pencil of about twenty long black setae. Outer dististyle about twice as long as broad, widest before midlength, setae long but relatively sparse. Inner dististyle with beak long and narrow, tip obtuse; lower beak and margin blackened, sclerotized; outer surface of basal half with numerous erect yellow setae. Aedeagus very long and stout, as common in the subgenus.

HABITAT. California (Calaveras County).

HOLOTYPE, alcoholic ♂, Buckeye Cace, September 4, 1961 (W. J. Gertsch); No. 1976. ALLOTYPE, ♀, Cave of the Catacombs, September 1, 1961 (R. E. Graham); No. 1893, in Alexander Collection. Type in American Museum of Natural History.

Named in honor of the collector, Dr. Willis J. Gertsch, distinguished student of the Arachnida. The fly is readily told from other generally similar species by having the tergal lobes of the male hypopygium entirely without spicules and in the long setal pencils on the ninth sternite. The most similar such species is *Tipula* (*Trichotipula*) *cazieri* Alexander, with other regional allies including *T.* (*T.*) *furialis* Alexander and *T.* (*T.*) *sayloriana* Alexander.

Tipula (*Yamatotipula*) *carsoni*, n.sp.

Size small (wing of male about 11 mm.); mesonotum gray, praescutum with four narrow brownish gray stripes that are narrowly margined with brown, pleura light gray, dorsopleural membrane yellow; antennae of male relatively long, flagellum black; wings weakly infuscated, prearcular and costal fields more yellowed; abdominal tergite yellow, with two broad dark brown longitudinal stripes; male hypopygium with the tergite produced into two flattened blades that are separated by a linear split, each blade on its inner and apical parts with slender spinoid setae; inner dististyle with beak large, outer margin strongly crenulated or scalloped; outer basal lobe a long narrow flattened blade, the apex truncate; gonapophysis a small slender blade.

MALE. Length about 9.5 - 10 mm.; wing 10.5 - 11.2 mm.; antenna about 4.2 - 4.3 mm.

Frontal prolongation of head yellowed, light gray pruinose above at base, nasus elongate; palpi with basal segment brown, remainder brownish black. Antennae with scape and pedicel obscure yellow; first flagellar segment elongate, brownish yellow, remainder of flagellum black, in the paratype, the extreme tips of the more proximal segments yellowed, outer segments uniformly blackened; segments feebly incised, much longer than the verticils. Head in front whitened, brownish gray behind, with indications of a darker median line; vertical tubercle small; setae of vertex short, black, of occiput longer, yellow.

Pronotum brownish gray, paler laterally. Mesonotal praescutum with humeral and lateral borders gray, disk with four narrow brownish gray stripes that are narrowly margined with brown, interspaces pale brown; scutum light gray, each lobe with two darker brown areas; scutellum brown, posterior border more yellowed; mediotergite light gray, posterior border narrowly darker; pleurotergite grayish brown, dorsal katapleurotergite clearer gray. Pleura light gray; dorsopleural membrane yellow. Halteres with stem brownish yellow, knob dark brown. Legs with coxae light gray; trochanters yellow; femora and tibiae brownish yellow, tips narrowly brownish black; tarsi passing into black. Wings weakly infuscated, prearcular field and cells *C* and *Sc* more yellowed, especially the latter; stigma brown, proximal end paling to yellow; a very restricted brown cloud over anterior cord; small obliterative areas before stigma and across base of cell *1st* M_2, the latter extending into apex of cell *R*; veins brown, more yellowish brown in the brightened areas. Venation: R_2 relatively long; cell *1st* M_2 small; cell M_1 deep, its petiole in cases to twice *m*.

Abdominal tergites with the restricted median ground yellow, with two broad dark brown sublateral longitudinal stripes, lateral margins paler yellow; sternites yellow; subterminal segments darkened to form a narrow ring; outer end of ninth segment, with the appendages yellowed. Male hypopygium with the tergite produced into two flattened blades, separated by a linear split, the apical and mesal parts of each blade with slender black spinoid setae. Outer dististyle unusually small, long-oval, with yellow setae; inner style much larger, the large beak yellow, gently arcuated, apex obtuse; outer margin crenulated or scalloped, forming about four lobes, with a strong pale seta in the notch of each crenulation, these gradually decreasing in size outwardly; face of beak conspicuously reticulated, with pale setae; outer basal lobe a long narrow flattened blade, apex truncate, the upper angle slightly produced. Phallosome with gonapophyses appearing as small slender flattened blades .

HABITAT. Newfoundland, Maine.

HOLOTYPE, ♂, Aspen Brook Rest Camp, Newfoundland, 300

feet, in swampy area along small lateral rills of brook at camp, July 17, 1961 (D. L. Carson). Paratype, ♂, Rangeley, Franklin Co., Maine, July 21, 1961 (A. E. Brower).

I take great pleasure in naming this fly for Mr. David L. Carson, companion on collecting trips to Alaska and Newfoundland, who has aided greatly in making known the crane flies of these areas. It most resembles species such as *Tipula* (*Yamatotipula*) *aprilina* Alexander, *T.* (*Y.*) *defecta* Walker, and *T.* (*Y.*) *sulphurea* Doane, differing from all in the structure of the male hypopygium, particularly the tergite and dististyles.

Tipula (*Platytipula*) *perhirtipes*, n.sp.

Closely allied to *Tipula* (*Platytipula*) *cunctans* Say; legs stout, very conspicuously hairy, including all segments from the femora through the third tarsal segment.

Female. Length about 17 mm.; wing 14 mm.; antenna about 3.1 mm.

Frontal prolongation of head light gray, clearer dorsally; nasus elongate; palpi brown, terminal segment short, black. Antennae with scape and pedicel light brown; proximal four segments of flagellum brownish yellow, their bases vaguely darker, outer segments passing into black; terminal segment small, subglobular. Head gray, vertex strongly infuscated.

Pronotum gray. Mesonotal praescutum gray, with three brown stripes; scutum gray, lobes patterned with brown; scutellum gray, darkened medially, parascutella and postnotum light gray. Pleura whitish gray, dorsopleural region yellowed. Halteres dark brown. Legs of female relatively short and stout; coxae whitish gray; trochanters yellow; femora and tibiae brownish yellow, tips narrowly blackened, more extensive on forelegs; tarsi passing into black; legs conspicuously hairy, with unusually long and abundant erect setae, including all segments with the exception of coxae and outer two tarsal segments. Wings brownish yellow, cells *C* and *Sc* dark brown, stigma yellowed; veins dark brown. Veins unusually glabrous, beyond cord with only two or three on vein R_{4+5}. Venation: Cell 1st M_2 relatively short, less than twice the petiole of cell M_1.

Abdomen obscure brownish yellow, patterned with darker, most evident as an interrupted median tergal stripe on proximal five segments, less evident elsewhere.

Habitat. Maine (Kennebec County).

Holotype, ♀, Vassalboro, in bog, September 30, 1961 (A. E. Brower).

Tipula (*Lunatipula*) *grahamina*, n.sp.

Mesonotal praescutum with five dark stripes, the lateral pair broad, intermediate three narrow, separated by delicate yellow lines; no nasus; femora brownish yellow, tips narrowly dark brown, claws simple, wings pale brown, stigma darker, whitened obliter-

ative areas before stigma and in cells *R*, 1st M_2 and M_3; male hypopygium with posterior border of tergite broadly emarginate, with a low median lobe at base of notch; aedeagus and apophyses generally similar in shape, appearing as slender blades; eighth sternite with posterior margin simple, the midregion with about 20 moderately long setae.

MALE. Length about 13-17 mm.; wing 12.5-17 mm.; antenna about 4.5-6.5 mm.

Frontal prolongation of head light brown, subequal to remainder of head; nasus lacking; palpi brown, terminal segment paler outwardly. Antennae with scape and pedicel yellow, flagellum brown, their segments shorter than the verticils. Head brown.

Pronotum brown. Mesonotal praescutum with broad sublateral brown stripes the median region with three narrow brown lines that are separated by equally narrow yellow vittae; scutal lobes dark brown, median area paler; scutellum brown, paler apically, with a vague darker central area; postnotum brown, lateral margins of mediotergite more yellowed, pleurotergite brownish yellow. Pleura chiefly dark brown; dorso-pleural region pale yellow. Halteres with stem pale, knob dark brown. Legs with fore and middle coxae yellow, restrictedly darkened at bases, posterior coxae more uniformly brown; trochanters yellow; femora brownish yellow, tips narrowly dark brown; tibiae and tarsi yellowish brown, terminal segment blackened; claws small,simple. Wings pale brown, stigma darker, cell *Sc* yellowed; white obliterative areas before stigma, outer end of cell *R* and bases of cells 1stM_2 and M_3; veins light brown. Venation: *Rs* about one-half longer than *m-cu*; petiole of cell M_1 about one-half longer than *m*.

Abdominal tergites brownish yellow, laterally with large brown spots; basal sternites more uniformly light yellow, outer segments and hypopygium dark brown. Male hypopygium with the tergite transverse, posterior border with a broad U-shaped emargination, with a small secondary median notch, beneath which is a low truncate sclerotized lobe; lateral lobes narrowly obtuse, margins virtually glabrous. Outer dististyle dilated outwardly, apex obliquely truncate, surface and margins with abundant setae, some very long; inner dististyle with beak narrowly obtuse, lower beak broadly so; posterior crest produced; outer basal lobe broad and conspicuous, tip obtuse. Phallosome with both the aedeagus and apophyses appearing as slender blades, narrowed to acute points, the former longer. Eighth sternite with posterior margin simple, without lateral lobes or armature; median region membranous, with about 20 moderately long setae.

HABITAT. California (Plumas and Shasta Counties).

HOLOTYPE, alcoholic ♂, Kloppenberg Cave, Plumas County, September 19, 1959 (R. E. Graham). PARATYPES, alcoholic ♂, Hall City Cave, Plumas County, August 1959 (R. de Saussure); No. 1285; alcoholic ♂, Samwel Cave, Shasta County, June 15,

1959 (R. E. Graham); No. 1162, in Alexander Collection. Type in American Museum of Natural History.

This interesting crane-fly is named for Mr. Richard E. Graham, Department of Mammalogy, American Museum of Natural History, who is conducting the present survey of the fauna of California caves. In the lack of a nasus and pattern of the mesonotal praescutum, the species agrees with *Tipula* (*Lunatipula*) *usitata* Doane, differing in further coloration and in all hypopygial details. *T.* (*L.*) *biunca* Doane likewise lacks the nasus but differs more decisively in hypopygial structure.

Tipula (*Lunatipula*) *productisterna*, n.sp.

Belongs to the *unicincta* group; mesonotal praescutum with three gray stripes, the interspaces brown, the intermediate pair more clearly so; antennae short, flagellum black; halteres yellowed, base of knob infuscated, legs brownish yellow, tips of femora and tibiae darkened, tarsi black, claws long-spined; wings strongly yellowish brown, scarcely patterned; abdomen yellow, tergites trivittate with dark brown, outer segments darker brownish yellow; male hypopygium with tergal lobes only slightly produced, rounded; ninth sternite produced into two long fingerlike lobes that are directed inwardly; outer basal lobe of inner dististyle long and fingerlike; phallosome with symmetrical apophyses; eighth sternite large and sheathing, outer lateral angles bearing a single powerful fasciculate bristle; median region of emargination with a glabrous depressed-flattened pale plate that is produced into two divergent blades.

Male. Length about 16 mm.; wing 17 mm.; antenna about 3.4 mm.

Frontal prolongation of head buffy yellow. Antennae relatively short; scape and pedicel yellow, flagellum black; flagellar segments very feebly incised, only slightly exceeding their longest verticils. Head brownish yellow, clearer yellow medially behind.

Pronotal scutum light brown, scutellum light yellow, clearer medially. Mesonotal praescutum with three brownish gray stripes, the interspaces clearer brown, best-indicated as long narrow lines on either side of the median stripe; posterior sclerites of notum brownish gray, central region of scutum narrowly yellowed. Pleura brownish gray; dorsopleural membrane light yellow. Halteres yellowed, including most of the knob, the base of latter infuscated. Legs with fore coxae infuscated, the remaining pairs and all trochanters more yellowed; femora and tibiae brownish yellow, tips narrowly darkened; tarsi black, claws long-spined. Wings strongly yellowish brown, darker on costal region, more yellowed on proximal half, stigma darker brown; obliterative areas conspicuous, yellowish white, crossing cell 1st M_2 into the adjoining cells; veins light brown. Venation: *Rs* long, more than three times $R_2 + {}_3$; petiole of cell M_1 shorter than *m*; distal section of Cu_1 strongly decurved at margin.

Abdomen yellowed, tergites trivittate with dark brown, the stripes narrowly interrupted by pale posterior borders, lateral margins broadly pale; outer segments, including the large hypopygium, darker brownish yellow. Male hypopygium with the tergite transverse, lateral lobes irregularly rounded, only slightly produced, median region completely divided. Ninth sternite on either side conspicuously produced into a fingerlike lobe, broad-based, bent inwardly; a further more ventral elongate lobe, its outer margin and apex with abundant short yellow setae. Outer dististyle a small oval blade on margin of the large inner style, this with the beak short-triangular; outer basal lobe narrowed into a fingerlike pale lobule. Phallosome symmetrical, the gonapophyses moderately large, spinelike, darkened, gradually narrowed into acute points. Eighth sternite large and sheathing, outer angles each with a single powerful fasciculate bristle; median region of emargination with a depressed-flattened pale plate, its outer margin produced into two divergent blades, separated by a U-shaped notch.

Habitat. Oregon (Harney County).

Holotype, ♂, Fish Lake Steens Mountains, 7,200 feet, July 14, 1962 (James Baker).

This interesting fly was taken by my long time friend James Baker, of Baker, Oregon, to whom I am indebted for many Tipulidae over the past several years. Other regional members of the *unicincta* group that have the tergal lobes only slightly produced include *Tipula* (*Lunatipula*) *mormon* Alexander and *T.* (*L.*) *rabiosa* Alexander, both of which have the hypopygial structure quite different, especially in the lack of the long fingerlike lobes of the ninth sternite as found in the present fly. Other species of *Tipula* with somewhat comparable elongate digitiform lobes have these on the basistyle rather than on the ninth sternite.

NOTE

Scissor-tailed Flycatcher in Death Valley, California

On May 3, 1962, the writer observed and collected a male scissor-tailed flycatcher *Muscivora forticata* at Furnace Creek Ranch in Death Valley, Inyo County, California. It was observed "fly-catching" among the mesquite growth whcih surrounds the "Ranch." This species increases the avian population of the below-sea-level region of Death Valley to 233 species (Wauer, Condor, 64:220-233). It is also the northeastern most record for the species in California and the first for the western portion of the Great Basin; along the eastern edge of the Sierra Nevada.

Roland H. Wauer, Zion National Park, March 20, 1963.

NEW DISTRIBUTIONAL AND HOST DATA FOR THE TICK *DERMACENTOR HUNTERI* BISHOPP

Elias P. Brinton[1] and Glen M. Kohls[2]

Published records indicate that the tick *Dermacentor hunteri* Bishopp has been collected from the bighorn sheep, *Ovis canadensis*, in Arizona (Bishopp, 1912; Cooley, 1938; Russo, 1956), Mexico (Cooley, 1938), and Nevada (Allen, 1962) and from the mule deer, *Odocoileus hemionus*, in Arizona (Russo, 1956). New distributional and host data from this little-known tick are presented below.

In April 1952, Miss Grace Grant, a student at Brigham Young University, collected a male tick of this species at the upper reaches of Beaver Dam Slope in southwestern Washington County, Utah. This locality is about five files due west of the Cliff Service Station on on Highway 91, between the Station and Terry's Ranch on Beaver Dam Wash. Apparently the tick was removed from the clothing since the collection data recorded it from man without any information that it was attached to the skin. On November 26 and 27, 1955, Dr. W. L. Jellison of the Rocky Mountain Laboratory removed two ticks, a male and a female, from his clothing while collecting mammals in the same general area. On June 22, 1961, Dr. D Elden Beck of Brigham Young University collected a female specimen from a cottontail rabbit, *Sylvilagus nuttallii grangeri*, taken in the upper part of Snow's Canyon, about seven miles north of St. George, Washington County, Utah.

In November and December 1962, Dr. Charles G. Hansen sent to the Brigham Young University Zoology and Entomology Dept. 351 males and 86 females of *Dermacentor hunteri* collected from bighorn sheep in the Desert Bighorn Sheep Reserve near Las Vegas, Nevada, and in January 1963 he sent 2 males and a female taken from a mule deer in the same area. This deer was also infested with the winter tick, *D. albipictus* (Packard).

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Cooley, R. A. 1938. The Genera *Dermacentor* and *Otocentor* in the United States, with studies in variation. National Institute of Health Bulletin No. 171, 89 pp.

Russo, J. P. 1956. The Desert Bighorn Sheep in Arizona. Wildlife Bulletin No. 1 Arizona Game and Fish Department. 153 pp. illus.

1. Brigham Young University, Provo, Utah.
2. Rocky Mountain Laboratory, National Institute of Allergy and Infectious Diseases, U. S. Public Health Service, Hamilton, Montana.

A NEW SPECIES OF CRANIOTUS (COLEOPTERA: TENEBRIONIDAE)

Vasco M. Tanner[1]

Within the last few years some intensive collecting in the southwestern part of the Great Basin, Arizona and northern Mexico has resulted in the accumulation of a large and interesting series of tenebrionid species. This study has to do with the description of the second known species of the rare genus *Craniotus*.

In 1851 John L. Leconte described a new genus and species[2] of Tentryiinae from a unique which was collected on the Colorado Desert of California. Leconte evidently proposed the name *Craniotus* because of the "horn-like" projections at the sides of the head anterior to the eyes. Other characteristics of the genus are: Clypeus round, shield shaped, intermediate lobe of the epistoma truncate, jaws bifid at tip; eyes almost transverse; antennae slender, third joint much elongated, the eleventh segment small and attached to the apex of the tenth which is much broadened; body convex, covered with fine setae; prothorax slender and round; sides wide without margins; scutellum elongate; epipleurae narrow and evident on the posterior part of the elytra; metathoracic coxae widely separated; femora and tibiae long, slender; tarsi with long hairs above and stiff spines beneath.

George Horn[3] observed that this "genus may be readily distinguished from all others of the tribe (Gnathosiini) by the very prominent triangular lateral lobes of the head. The epipleurae and the elytra are connate without trace of suture."

Col. Casey believed this singular genus was most closely allied to the old world Adesmiini; also that it resembles the American *Edrotes* in many respects. He comments as follows: "In *Adesmia* the eyes are much more finely faceted the head and mandibles are almost similar, except that the front is not dilated at the sides and the mentum not emarginate at base, and the eleventh antennal joint is free, though very small. The coxae and metasternum are almost exactly as in *Craniotus*, but the posterior are still more widely separated, almost globular in form and approach the sides of the body very closely."

Specimens of *Adesmia* have not been seen by the writer, but several species of the genra *Edrotes* and *Triorophus* have been studied and comparisons made with *Craniotus*. There are some external body resemblances of *Craniotus* with the above mentioned genera, but there is no agreement in the genitalia structures. If

1. Contribution No. 183 from the Dept. of Zoology and Entomology, Brigham Young University, Provo, Utah. Paratype specimens, of this study, were collected by field workers of the Brigham Young University under the Atomic Energy Commission Contract AT (11-1) 786.

2. Leconte, John L., Description of new species of Coleoptera from California, Annals Lyc. N.H.N.Y. Vol. V, pp. 125-216, pl. 1851.

3. Horn, George H., Revision of the Tenebrionidae of America, North of Mexico. Trans. Am. Phil. Society. Vol. XIV, Pt. II.

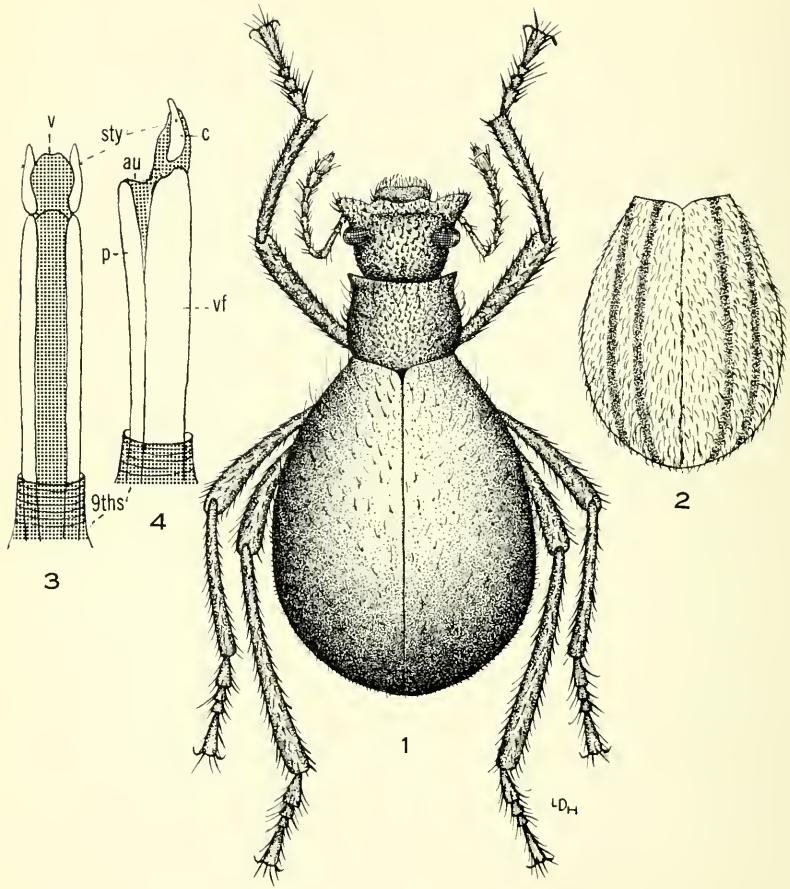

Fig. 1 Dorsal view of the female of *C. blaisdelli.* Fig. 2 Elytral pattern of *C. pubescens.* Fig. 3 Ventral view of genitalia of *C. blaisdelli.* Fig. 4 Lateral view of *C. blaisdelli.*

other characters than those used by early workers are considered in making decisions as to relationships of genera. tribes and subfamilies, we will need to abandon Col. Casey's conclusions in the light of present morphological findings. The writer has long contended, 1927[4], that more attention must be paid to the internal as well as the external morphology of the beetles. Blaisdell's work on the genitalia of the Tenebrionidae has added materially to the value of his studies of this family. In 1934[5] he commented as follows on the necessity of shifting *Craniotus* to the subfamily Asidinae: "The study of the genitalia of the Tenebrionidae indicates very definitely

4. Tanner, Vasco M. 1927., A Preliminary Study of the Genitalia of Female Coleoptera. Trans. Am. Ento. Soc. Vol. LIII, 5-50. 14 plates.
5. Frank E. Blaisdell, Sr., 1934. Studies in the Genus Auchmobius (Coleoptera: Tenebrionidae). Trans. Am. Ento. Soc. LX, 223-264. Plates XVI, XVII, and XVIII.

that changes should be made in the taxonomic sequences of subfamilies and tribes. . . . The Craniotini possess genitalia wholly Asidine in character and should precede the Asidini in our lists." Again Blaisdell, 1939[6], contends that: "The Asidinae possess distinctive primary sexual characters, the typical characters are described above and figured in Plate V. The species *Craniotus pubescens* Leconte heretofore placed after Edratini and before Zopherini in our lists. belongs to the subfamily Asidinae, Tribe Craniotini. Its genital characters being distinctly of the type found in that subfamily. The author has reported this fact in a previous publication."

Not only do species of *Craniotus* agree in general with the female genitalia structures of the Asidinae, but there is also an agreement in the type of antennae, mentum, eyes, and position of the closed coxal cavities. I am, therefore, of the opinion that in this instance the female genitalia (fig. 3-4) of *C. blaisdelli* as well as external body characters are more closely related to Asidini than Edrotini and that *Craniotus* and species should be placed in the tribe Craniotini in the subfamily Asidinae.

Craniotus blaisdelli Tanner, n. sp.

Figs. 1-4

FORM robust, two times as long as wide. Color deep black, luster dull to slightly shining.

HEAD small in size, projections at the sides of the head anterior to the eyes extend beyond one third the width of the head; frons depressed between the projections and the clypeal area; clypeus slightly emarginate; epistoma punctures discrete, small, irregular, each bearing a short black seta. Eyes transverse, not emarginate, larger dorsally. Antennae slender, third joint as long as the fourth and fifth combined, in length not extending to the pronotal base; the eleventh segment small, attached to apex of tenth.

PRONOTUM about one-sixth wider than long, sides without margins, disk convex, anterior angles acute, *surface* with irregularly placed papilliform structure, each bearing a decumbent brownish colored seta. Base broadly truncate, scutellum elongate.

ELYTRA one third longer than wide, base equal to that of the pronotum; humeri obsolete, sides broadly arcuate, disk moderately convex; arcuately precipitous at apex; surface devoid of striae; small punctures from which arise short stiff black setae; luster dull to more or less shining, connate, the suture, however, is distinct. Epipleurae without a trace of a suture.

LEGS long, especially the tibiae of the metathoracic legs; coxa closed and widely separated. First and second abdominal sternites about equal, in width, punctured and with black short erect setae.

GENITALIA of the female, figs. 3-4, of the elongate type, rather

6. Frank E. Blaisdell, Sr., 1939. Studies in the Relationships of the Subfamilies and Tribes of the Tenebrionidae, Based on the Primary Genital Characters also descriptions of new species. (Coleoptera.) Trans. Am. Ento. Soc. LXV, 43-60, Plates IV and V.

heavily sclerotized valvifer; coxite small, black, with obscure stylus; ninth segment membranous, acting as a sheath for the retracted genital organ. The female genitalia of *Pelecyphorus semilaevis* is an elongate type similar in structure to *C. blaisdelli.*

Measurements: length 10-13 mm; width 5-6 mm.

Type: Female, collected in Inyo Mountains, California, April 18, 1949 by Owen Bryant.

Paratypes: 1-♀, collected by field workers of the Brigham Young University, Nevada test site Ecology Project, 12.5 miles N.N.E. of Mercury, Nevada, in the *Larrea-Franseria* Community, Nov. 1961; 1-♂ collected 9.3 miles west of Mercury in the *Larrea-Franseria* Community, Dec. 1961; 1-♀ collected 32.5 miles north of Mercury in a *Coleogyne* Community, Nov. 1960.

Type and paratypes are in the author's collection at Brigham Young University. One paratype deposited in the entomological collection of the California Academy of Sciences at San Francisco.

I am pleased to dedicate this species to the memory of Dr. Frank E. Blaisdell, Sr., one of this country's most renown authorities on the Tenebrionidae.

Remark:—*Craniotus blaisdelli* is a larger species than *pubescens.* The elytral covering of *blaisdelli* consists of sparse, short black setae, devoid of striae and with a more or less dull luster yet with a shining surface. The elytra of *pubescens*, fig. 2, has three rather distinct lines or areas on either side of the suture which are covered with brownish decumbent thickly placed setae. These areas are separated by small spaces devoid of setae. The head and thorax of *pubescens* is also thickly covered with brownish decumbent setae. The prothorax is more round and convex with numerous deep punctures.

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